Biology and Population Dynamics of Sacramento Splittail (*Pogonichthys macrolepidotus)* in the San Francisco Estuary: A Review

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Abstract

The Sacramento splittail (*Pogonichthys macrolepidotus*) is a cyprinid fish endemic to the Central Valley of California with a range that centers on the San Francisco Estuary. It is listed as a threatened species by the U. S. Fish and Wildlife Service. Splittail live 7-9 years, can tolerate a wide range of environmental conditions, and have high fecundity. Typically, adults migrate upstream in January and February and spawn on seasonally inundated floodplains in March and April. In May the juveniles migrate back downstream to shallow, brackish water rearing grounds, where they feed on detritus and invertebrates for 1-2 years before migrating back upstream to spawn. Seven long-term sampling programs in the estuary indicate that the splittail population is maintained by strong year classes resulting from successful spawning in wet years, although some spawning occurs in all years. Modeling shows them to be resilient, but managing floodplains to promote frequent successful spawning is needed to keep them abundant. Additionally, it is important to provide safe migration corridors between spawning and rearing grounds as well as abundant high-quality brackish water rearing habitat. Key research needs are (1) to examine how the timing, magnitude, and duration of high flows contribute to the generation of strong year classes, (2) to describe differences in YOY survival on the floodplain and in river margins from hatching to down-river migration, and (3) explore the possible trophic effects of new invaders such as the overbite clam and Siberian prawn.

Keywords

Sacramento River, Sacramento-San Joaquin Delta, Sutter Bypass, Yolo Bypass, floodplain, endangered fishes, Cyprinidae.

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1.0 Introduction

The Sacramento splittail (*Pogonichthys macrolepidotus*) is a cyprinid fish endemic to the Central Valley of California with a range that centers on the San Francisco Estuary. It is listed as a threatened species by the U. S. Fish and Wildlife Service (USFWS) and is considered to be a Species of Special Concern by the California Department of Fish and Game (CDFG). Therefore, managing processes and habitats in ways that favor splittail is a high priority of the CALFED Ecosystem Restoration Program Plan (ERPP) and the Multi-species Conservation Strategy. It is also necessarily a focus of various modeling efforts to predict the impact of changing flow regimes on endangered species. Therefore, the purpose of this paper is to:

(1) summarize what is known about the biology of Sacramento splittail, including (a) history and taxonomy, (b) distribution and abundance, and (c) ecology and life history;
(2) provide a conceptual model of splittail life history;
(3) list uncertainties in our knowledge of splittail, expressed as a series of hypotheses;
(4) present a simulation model of splittail population dynamics to explore limiting factors, based on present knowledge;
(5) discuss potential effects of climate change and earthquakes on splittail;
(6) discuss management and restoration options.

The peer-reviewed literature on splittail is limited, so this review depends heavily on unpublished data from various agency surveys, reports in the grey literature, and the on-going studies of three of the co-authors: T. Sommer, R. Baxter, and P. Moyle. While an enormous amount has been learned about splittail in the past few years, we are still in the hypothesis stage as to limiting factors. Some of the key hypotheses relating to splittail management need to be tested with both hydrodynamic models and large-scale field experiments conducted in association with habitat restoration projects. Such tests provide an excellent opportunity for the application of adaptive management. Therefore a major purpose of this paper is to provide background and guidance for designing modeling and management experiments.

2.0 History and Taxonomy

2.1 Official History

Splittail evolved in the Central Valley over millions of years. They were harvested in small numbers by Native Americans for a few thousand years. Their formal history in relation to Western culture, however, does not begin until 1854. The following are milestones in their official history:

1854. W. O. Ayres, a physician, formally describes, in a San Francisco newspaper, Sacramento splittail as a new species based on fish purchased from a local market.

1908. C. Rutter finds splittail to be widespread in the Central Valley, from the Sacramento River at Redding to the lower Merced River.

1931. L. A. Walford describes splittail as being taken in small numbers in commercial fisheries.

1963-64. A one-year CDFG survey captures 536 splittail in the Delta and 291 in Suisun Bay (mostly adults). The study finds them to be common and widely distributed but devotes only 10 lines of text to their biology in the published report (Turner and Kelley 1966).

1973. J. Hopkirk describes the Clear Lake splittail as a separate species (*P. ciscoides*) but it is apparently already extinct by the time the description is published.

1974. M. Caywood finishes his M.S. thesis on splittail in the Delta, the first study of its life history, which remains unpublished.

1983. The first peer-reviewed life history study, based on the Suisun Marsh population, is published (Daniels and Moyle 1983).

1989. January. USFWS included splittail as a category 2 candidate species for possible listing as endangered or threatened (Annual Notice of Review 54 FE 554).

1989. The splittail is listed as a Species of Special Concern by CDFG (Moyle et al. 1995).

1992. Status and Trends Report from San Francisco Estuary Project documents widespread decline of native species in estuary, including splittail (Herbold et al. 1992).

1992. November. USFWS receives a petition from G. A. Thomas of the Natural Heritage Institute and eight co-petitioning organizations to list splittail under the Endangered Species Act and to designate critical habitat based on information eventually published in Meng and Moyle (1995) (Natural Heritage Institute 1992).

1993. March. USFWS initiates review of splittail for possible listing.

1994. January. USFWS proposes to list splittail as threatened (USFWS 1994a) but listing is delayed by three extensions (USFWS 1995) of the comment period and a one year moratorium on all federal endangered species listings and budgetary constraints that precluded work on listing from April 1996 to April 1998.

1994. March. At the request of USFWS, a recovery plan for seven declining species, including splittail, in the Bay-Delta estuary is completed in one year (USFWS 1994b). Final report not released by USFWS until November 1996.

1996. Laboratory studies on splittail reveal they are remarkably tolerant of wide ranges of temperature, salinity, and dissolved oxygen and are strong swimmers (Young and Cech 1996).

1997. A major analysis of splittail biology demonstrates the ability of populations to respond quickly to favorable conditions (Sommer et al. 1997).

1998. December. A federal court orders USFWS to take action on splittail listing, in response to a suit by Southwest Center for Biological Diversity.

1999. February. USFWS lists splittail as threatened species (USFWS 1999).

2000. June. In response to a lawsuit by San Luis and Delta-Mendota Water Authority, a federal court determines that the splittail listing is not justified and orders the USFWS to reverse the listing. The legal status of the splittail is still under review.

2001. January, May, August. Comment period for listing of splittail as a threatened species opened again by USFWS, thrice.

2002. March and October. Comment period for listing of splittail as a threatened species was re-opened twice by USFWS.

2.2 Description and Taxonomy

The Sacramento splittail is described by Moyle (2002) as follows:
"This large (to over 40 cm SL) cyprinid is readily recognized by the enlarged upper lobe of the tail, tiny barbels (sometimes absent) at the corners of the slightly subterminal mouth, and small head (head length divisible into body length less than 4.5 times) on an elongate body. The dorsal rays number 9-10; pectoral rays, 16-19; pelvic rays, 8-9; anal fin rays, 7-9; lateral line scales, 57-64 (usually 60-62); and gill rakers, 14-18 (usually 15-17). The pharyngeal teeth, usually 2,5-5,2, are hooked and have narrow grinding surfaces. The inner tooth rows are very small. Live fish are silvery on the sides, but become duller in color as they grow larger. The back is usually dusky olive gray. Adults develop a distinct nuchal hump on the back. During the breeding season, paired, dorsal, anal, and caudal fins are tinged with red-orange, and males become darker colored, developing tiny white tubercles on their heads and on bases of the fins."

The Sacramento splittail is one of the most distinctive cyprinids in North America, as indicated by its assignment to a genus shared only with the extinct Clear Lake splittail (*P. ciscoides*) from Lake County. Although it was suspected to be more closely allied to Eurasian cyprinids than to other North American species (Howes 1984), zoogeographic and genetic evidence affirm its ancient ties to other endemic cyprinids of California (Moyle 2002).

3.0 Trends in Distribution and Abundance

3.1 Distribution

Sacramento splittail are endemic to the sloughs, lakes and rivers of the Central Valley. In the Sacramento Valley, they were found in early surveys as far up the Sacramento River as Redding (below the Battle Creek Fish Hatchery in Shasta County), in the Feather River as high as Oroville, and in the American River to Folsom (Rutter 1908). Today they are found most frequently in the Sacramento River below the mouth of the Feather River and become increasingly rare in an upstream direction, particularly during summer and fall (Table 1). A few individuals have been found annually in the Sacramento River at Red Bluff Diversion Dam (river km [rkm] 391), at Hamilton City (rkm 331), at the entrance to the Glenn Colusa irrigation diversion (rkm 329) and at the mouth of Big Chico Creek (rkm 312) (Baxter et al. 1996, Sommer et al. 1997, Baxter 1999a, 2000, R. Baxter, unpublished data). While individuals of various ages have been caught at times other than spring (when spawning occurs), evidence for self-sustaining populations outside the estuary and lower Sacramento River is weak. In high outflow years, adult splittail migrate upstream and become abundant in winter and spring (January-April) in the lower Sacramento River (to above Verona, rkm 129, near the mouth of the Feather River) and in the Sutter and Yolo Bypasses (Sommer et al. 1997, Baxter 1999a). Large numbers of larvae and juveniles are produced and move downstream. In low outflow years fewer adult splittail appear to migrate, but based on presence of larvae and juveniles, spawning still takes place on the lower Sacramento River margins and may even shift higher to the Colusa (rkm 232), Princeton (rkm 296), Ord Bend (rkm 262) regions (Baxter 1999a).

In the San Joaquin basin, archaeological evidence indicates valley floor populations existed in lakes Tulare and Buena Vista, where they were harvested by native peoples (Hartzell 1992, Gobalet and Fenenga 1993). Today, splittail may ascend the San Joaquin River to Salt Slough (rkm 208) during high outflow years (Baxter 1999a, 2000). During low outflow years, splittail are uncommon in the San Joaquin River downstream of the Tuolumne River confluence

(USFWS unpublished data) and rare upstream, although individual fish were captured in 2001 and 2002 near the mouth of Mud Slough (R. Tibstra, personal communication, see "Notes"). Spawning apparently occurred in the lower Tuolumne River during wet years in the 1980s and 1990s, because both adults and juveniles were observed at Modesto, 11 km upstream from the river mouth (T. Ford, personal communication, see "Notes").

In the San Francisco Bay area, Snyder (1905) reported catches of splittail from southern San Francisco Bay and at the mouth of Coyote Creek in Santa Clara County, but they are now rare there (Leidy 1984, Table 1). In high outflow years splittail are occasionally captured in the low salinity lens that forms along the margins of Central and South bay (CDFG Bay Study, unpublished data). In the estuary, splittail are largely confined to the Delta, Suisun Bay, Suisun Marsh, lower Napa River, and lower Petaluma River. The Petaluma River estuary apparently supports a self-sustaining population, but it is not clear if the same is true of the Napa River. Splittail are rare or absent from Napa Marsh during droughts, but are common to abundant in normal and wet years. In the Delta, they are most abundant in the north and west portions when populations are low but are more evenly distributed in years with high reproductive success (Turner and Kelley 1966, Sommer et al. 1997). The distribution of adults in the estuary suggests that brackish water may characterize optimal rearing habitat for older fishes (Sommer et al. 1997). Occasionally, splittail are caught in San Luis Reservoir which stores water pumped from the Delta, and a single specimen has been reported from Silverwood Reservoir, at the southern end of the California Aqueduct (Swift et al. 1993).

Table 1. Maximum extent of splittail distribution in major rivers as indicated by location of splittail collections (based on Sommer et al. 1997). NA indicates specific information is not available. Distance is river kilometer from the mouth of the river. "Present" indicates the exact location is not known but that splittail were documented as being in the river system.

River System	**Historical** [a]	**1970s** [b]	**Mid 1990s** [c]	**Recent**	**Dam** [d]
Sacramento	483	387	331	391 [e]	391
Feather	109	Present	94	68 [f]	109
American	49	37	19	NA	37
San Joaquin	Widespread	Present	201	218.5 [g]	295
Mokelumne	NA	25	63	96 [h]	63
Napa	NA	21	10	28.5 [i]	None
Petaluma	NA	25	8	27.5 [j]	None
Coyote Creek	NA [k]	NA	1 [l]	NA	16

[a]Rutter 1908
[b]Caywood 1974
[c]Sommer et al. 1997
[d]River km to first dam:

Sacramento – Red Bluff Diversion Dam
Feather – Orville Dam
American – Nimbus Dam
San Joaquin – Sack Dam
Mokelumne – Woodbridge Dam

Napa – Not dammed
Petaluma – First dam removed in 1994
Coyote Creek – Standish Dam
[e]D. Killiam, personal communication, see "Notes."
[f]B. Cavallo, personal communication, see "Notes."
[g]Baxter 1999a
[h]J. Merz, personal communication, see "Notes."
[i]Napa River Fisheries Monitoring Program, Annual Report 2001
[http://www.napariverfishmonitoring.org/reports/reports.html]
[j]B. Cox, personal communication, see "Notes."
[k]Aceituno et al. 1976 (cited in CDWR 1999).
[l]M. Stevenson, personal communication, see "Notes."

Conclusions. Splittail once occurred in low-elevation habitats throughout the Sacramento and San Joaquin Valleys, but were most abundant around the estuary. Historically, both valleys had abundant lake, slough, backwater, and floodplain habitat that likely supported all life history stages of splittail. Today most adult and juvenile rearing habitat appears to be in the tidal upper estuary, including Suisun Bay, especially in brackish water, and the Petaluma River estuary. Early fisheries suggested that splittail had strong seasonal migrations (Walford 1931). During wet years today, high outflow attracts adult splittail long distances upstream to spawn and allows juvenile rearing in upstream habitats. In virtually all dry years, some spawning occurs upstream of the City of Sacramento.

3.2 Abundance

The historic abundance of splittail is not known but they were harvested by Native Americans and by commercial fisheries in the 19th and early 20th centuries. They were apparently common and widely distributed in the estuary through the early 1960s but evidence is anecdotal because systematic fish sampling did not begin until 1963. Although there is no program that systematically estimates total splittail abundance, there are seven sampling programs that capture splittail frequently enough to develop indices of abundance. The programs are (1) CDFG Summer Townet Survey, (2) CDFG Fall Midwater Trawl Survey, (3) USFWS Chipps Island trawl survey, (4) U. C. Davis Suisun Marsh trawling and seining surveys, (5) USFWS Beach Seine Survey, (6) CDFG San Francisco Bay trawling survey, and (7) fish salvage operations at CVP and SWP pumps in the south Delta. None of these surveys or the indices calculated from them were designed specifically for splittail so the results of each have to be interpreted with caution, although they have all been used in analyses of splittail population trends (e.g., Meng and Moyle 1995, Sommer et al. 1997, Baxter 1999b).

Summer Townet Survey. The Summer Townet Survey by CDFG was started in 1959 to provide an index of striped bass (*Morone saxatilis*) abundance. It uses oblique tows in mid-channel sites located throughout the Delta, Suisun Bay, and San Pablo Bay to sample young-of-year (YOY) fish twice monthly. Starting and ending dates vary from year to year. Data for species other than striped bass were not regularly recorded until 1962, nor were they recorded in 1966, 1967, and 1968. The survey catches low numbers of YOY splittail, presumably because it focuses on pelagic habitats while splittail are primarily benthic (CDWR and USBR 1994). Also, historically variable starting dates did not always coincide with peak YOY numbers. Not surprisingly, splittail catch varies widely and the index reflects only gross changes in YOY splittail abundance. The index reached its maximum value in 1982, had lower peaks in 1963, 1978, 1986, 1995, and 1998, and was low during most years of the 1987-1992 drought (Figure 1).

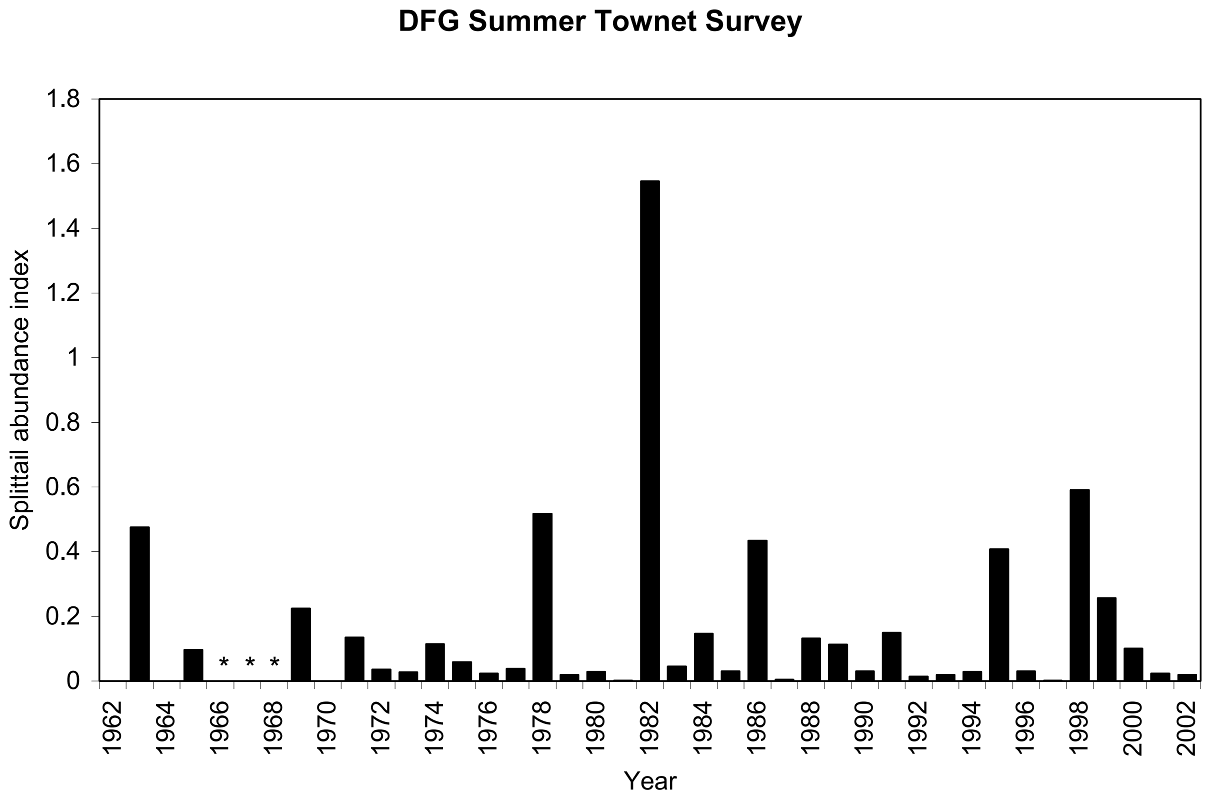


Figure 1. Splittail abundance index (average splittail catch per tow) from the CDFG Summer Townet Survey. An asterisk (*) denotes years in which no sampling occurred.

Fall Midwater Trawl Survey. The Fall Midwater Trawl Survey (FMWT) was started in 1967 by CDFG to sample striped bass, but other species were recorded in most years. This monitoring program currently samples 100 sites from San Pablo Bay in the west to Rio Vista on the lower Sacramento River and to Stockton on the San Joaquin River (Sommer et al. 1997). Data are collected in September, October, November, and December using a midwater trawl with a 3.7 m^2 mouth. Unlike the summer townet survey, the FMWT survey catches all size groups, although large fish are more likely to evade capture. Catches of splittail are generally low because of the benthic orientation of splittail and because splittail use shallow edge habitats to a higher degree than open channels. The FMWT does not sample edge waters and the proportion of samples in shallow-water stations varies by region: 20 of 35 stations in San Pablo Bay, 1 of 18 in Carquinez Strait, 8 of 25 in Suisun Bay/Marsh, and 1 of 38 in the Delta. A monthly abundance index for splittail is calculated by grouping the samples by area (17 areas) and then calculating an area-weighted average catch from each area; the index is the sum average of these area-weighted mean catches (Sommer et al. 1997). The annual FMWT Index is the sum of the four monthly indices (Sommer et al. 1997). Splittail lengths were not recorded until 1975 so YOY abundance could not be separated from that of other age classes until then.

The annual total abundance indices peaked in 1967, 1982, 1983, 1995, and 1998 and were low during most of the 1987-1992 drought (Figure 2). Peaks in abundance are largely a reflection of high catches of YOY, especially in recent years. For example, 98% of the total catch for 1995 was YOY, as was 94% of the total catch for 1998. In years immediately following high YOY catches (e.g., 1983, 1987, 1996, 1999), the proportion of yearlings and older fish (non YOY) increased predictably, reflecting the successful cohort.

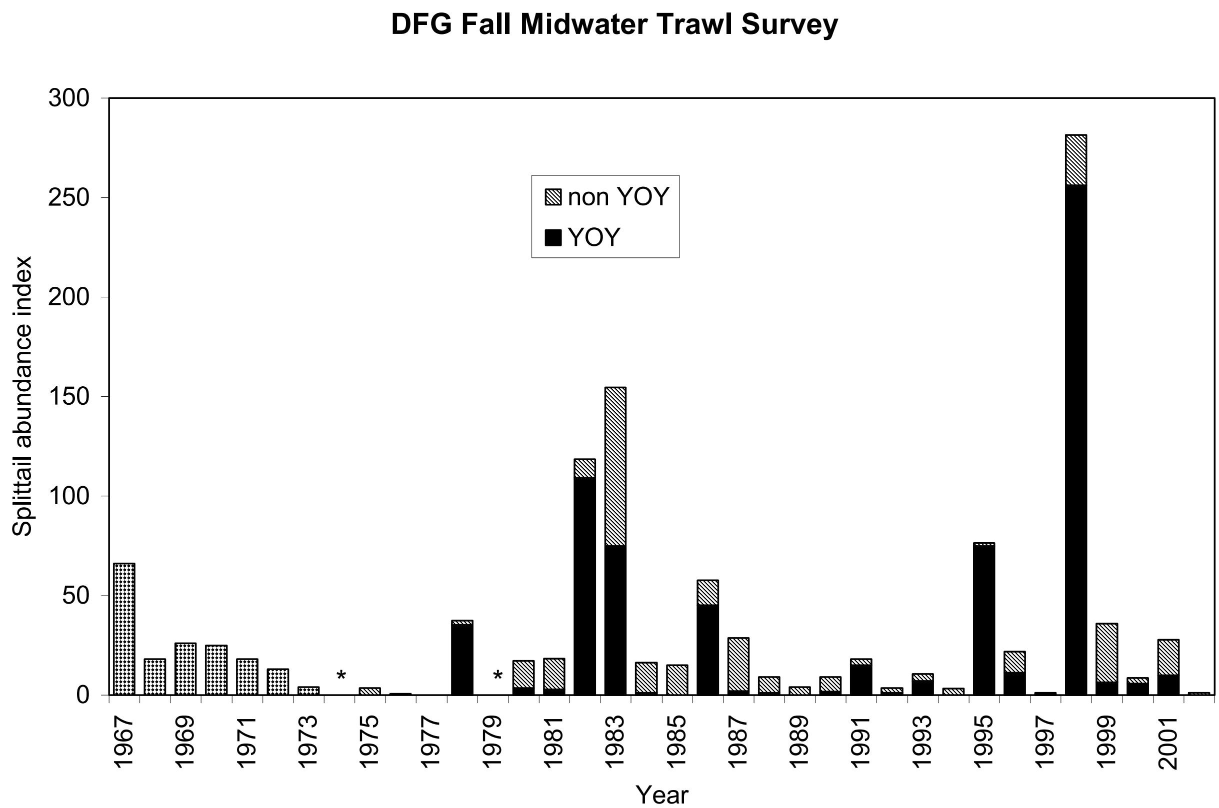


Figure 2. Splittail abundance index (see text for calculations) from the CDFG Fall Midwater Trawl Survey. Checkered boxes (1967-1973) indicate years in which fish were not classified into age groups. An asterisk (*) denotes years in which no sampling occurred.

Chipps Island Survey. The USFWS trawls for juvenile salmon in the deep-water channel near Chipps Island at the western terminus of the Delta. A midwater trawl is towed at the surface for 20 minutes per haul, there are 10 hauls per sampling day, and the number of sampling days per week is variable (Sommer et al. 1997). For splittail, data were compiled to produce an index based on the catch per hour of trawling for the months of May and June combined (Sommer et al. 1997). Age-specific indices (based on length) are somewhat speculative prior to 1994 due to high numbers of unmeasured fish, and are not presented here. In July 1995, a 25 mm FL minimum criterion for cyprinid identification and data inclusion was adopted.

The total catch per hour peaked in 1978 and fluctuated at intermediate levels for much of the next decade. Catches were low during the 1987-1992 drought and remained low until 1995, when the index reached its highest peak of the study. In subsequent years abundance fluctuated at or above drought-period levels, with small peaks in 1998 and 2000 (Figure 3). Recent abundance peaks were mainly due to YOY.

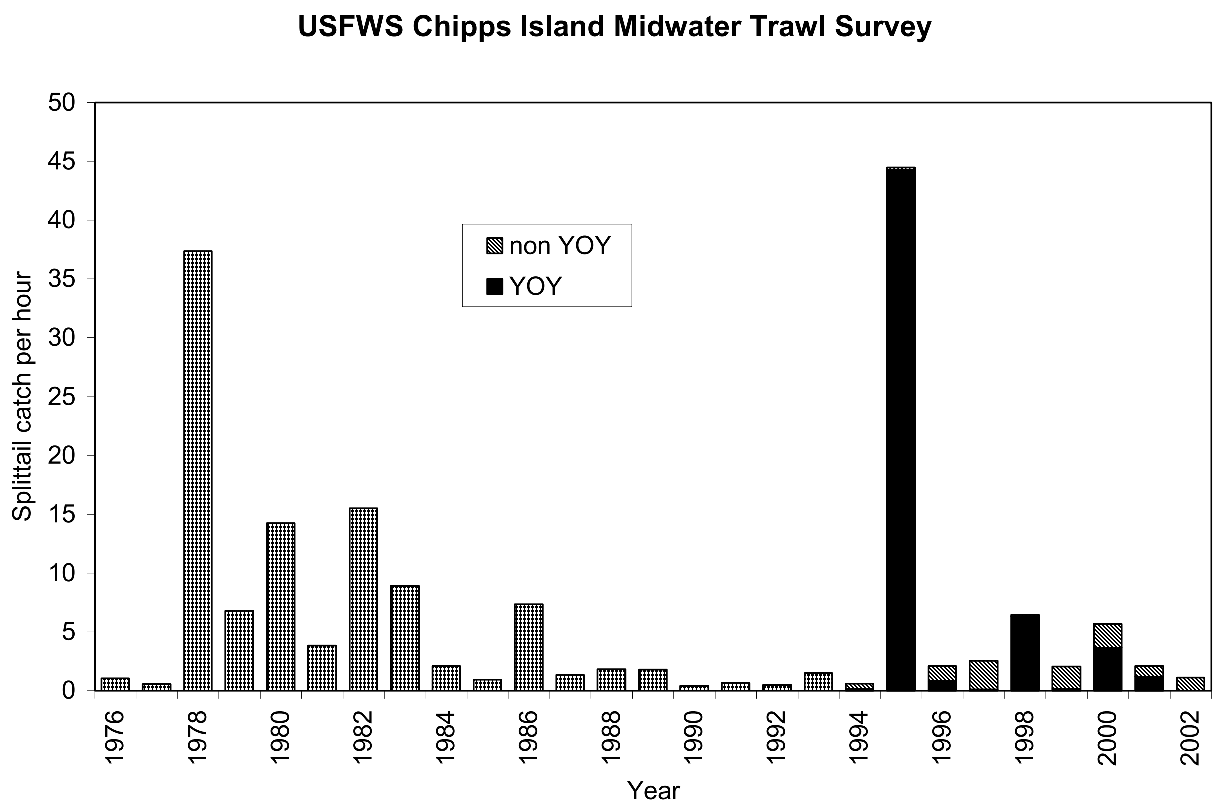


Figure 3. Splittail catch per hour from the USFWS Chipps Island Midwater Trawl Survey. Checkered boxes prior to 1994 represent total catch; beginning in 1994 fish were reliably classified into age groups.

Suisun Marsh Survey. The Suisun Marsh Survey is conducted by the University of California, Davis as part of a study of the ecology of the entire fish community of the marsh that started in 1979 (Moyle et al. 1986). The program is funded by CDWR through the Interagency Ecological Program to determine if management actions in Suisun Marsh are affecting fish communities. The program currently includes monthly sampling at 21 sites in nine sloughs (Matern et al. 2002). The primary gear is an otter trawl which drags along the bottom and samples much of the water column in the shallow sloughs. Two sites are also sampled each month using a beach seine (data not presented here). Catches of most species, including splittail, are dominated by YOY (Matern et al. 2002) but the sampling also consistently catches larger fish, so this program is the most thorough for splittail of the various sampling programs. Splittail collection in Suisun Marsh is enhanced by reduced gear avoidance in narrow, relatively shallow sloughs sampled as part of the monthly survey. In such conditions, the net samples a larger proportion of the channel cross-sectional area than in any other survey. Larger sized fish, however, presumably become progressively less vulnerable to the trawls. A monthly abundance index was calculated as mean catch per trawl. The annual abundance index (Figure 4) was calculated as the mean of the monthly index values (Sommer et al. 1997).

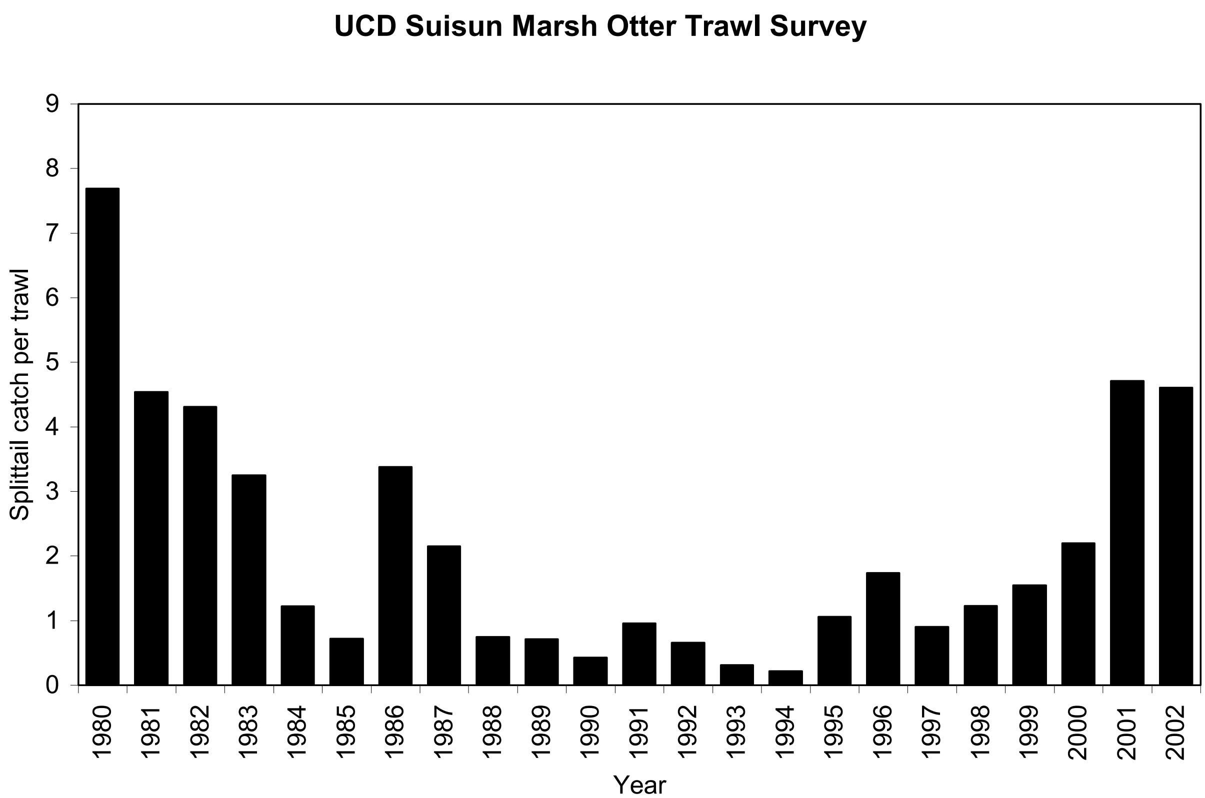


Figure 4. Splittail catch per trawl from the UCD Suisun Marsh Otter Trawl Survey.

The Suisun Marsh otter trawling data show splittail to be common through 1987, then relatively uncommon during the drought and through 1994. Beginning with the recruitment of the strong year class of 1995, catches increased and have returned to historic levels in 2001 and 2002. The recent population rebound seems to be due to an influx of YOY from upstream, rather than from spawning within the marsh itself. Two main lines of evidence support this hypothesis. First, an annual Suisun Marsh splittail YOY index (Figure 5) was developed by using a month-specific YOY size criterion (S. Matern, unpublished data) which was used to calculate YOY per trawl for the period April-December (to avoid having two year classes per calendar year). When this index is compared to the total catch index, it shows that peaks in YOY (e.g., 1982, 1986, 1995, 2000) are usually echoed in high overall catches in the same year and for 1-2 years thereafter, suggesting that YOY splittail remain in the marsh after their first year. Additional support is found in the observation by Matern et al. (2002) that seasonally changing environmental factors within Suisun Marsh did not affect post-recruitment splittail abundance.

The second line of evidence is the absence of abundant splittail larvae within the marsh. The UCD program sampled ichthyoplankton weekly each spring from 1994 to 2002 using a 505 µm mesh net towed just below the surface (Meng and Matern 2001). There were 61 splittail larvae collected in 1995 (mostly in April) and catches were < 20 for all other years (R. Schroeter, UCD, unpublished data). These low catches of larval splittail, especially in years with high catches of juveniles, support the hypothesis that Suisun Marsh is more important to splittail as a rearing area than a spawning area. Recent modeling studies indicate that the Yolo Bypass, a major spawning and nursery area, is hydrologically connected to Suisun Marsh (N. Monsen, Stanford University, unpublished data) so juvenile trends in the marsh are likely heavily influenced by upstream production. However, this picture is clouded by the observation that recent strong cohorts of juveniles (1995, 1998) found in other studies were not as obvious in the Marsh samples. In extremely high outflow years, such as 1995 and 1998, much of the splittail production from the bypasses may have been swept past Montezuma Slough (the main upstream entrance to Suisun Marsh) and reared in Honker Bay, Grizzly Bay and the shallows of Suisun Bay instead.

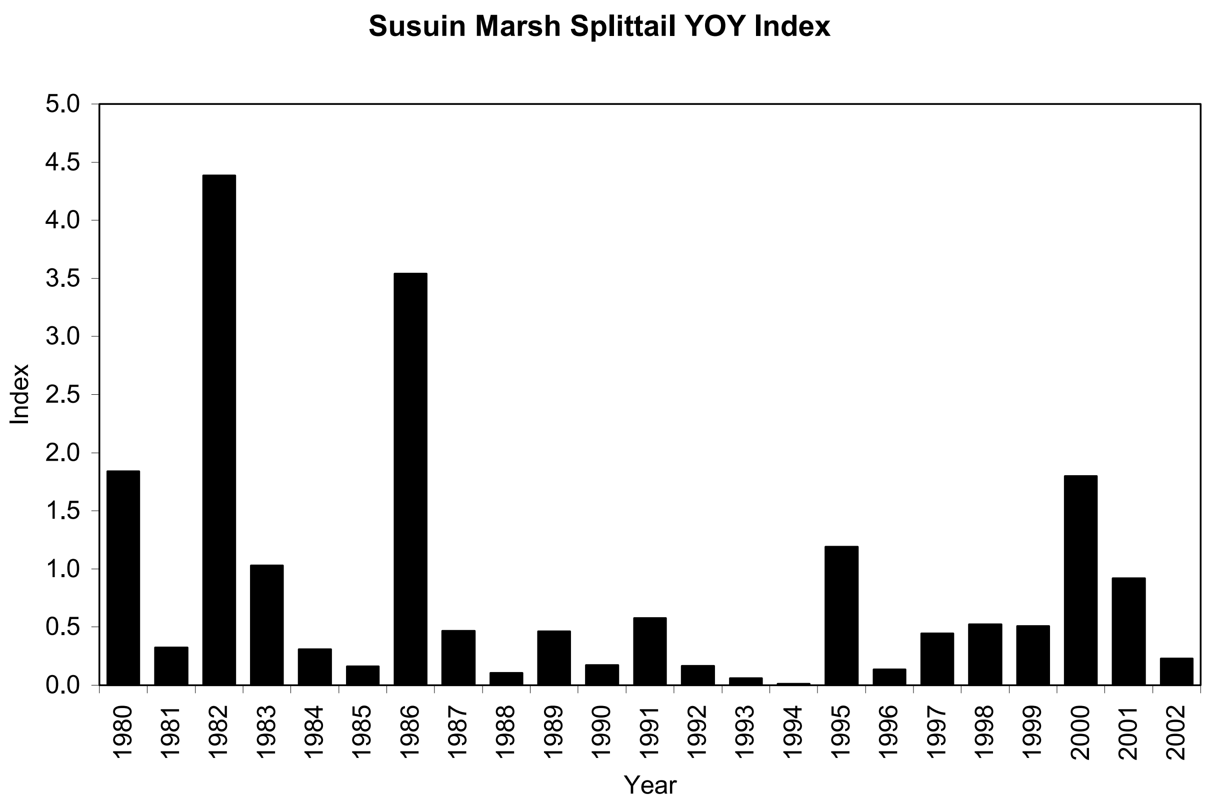


Figure 5. Splittail YOY index (April-December; see text for calculations) from the U. C. Davis Suisun Marsh Otter Trawl Survey.

U. S. Fish and Wildlife Beach Seine Survey. The USFWS conducts a regular beach seine survey at 23 stations. The stations are scattered around the Delta, extending south of Stockton, including the mouths of the Mokelumne and San Joaquin rivers, and up the Sacramento River to the confluence of the American River. Sampling is conducted with a 15 m beach seine in low-velocity areas near the shoreline, in contrast to other sampling programs that sample in deeper water (Sommer et al. 1997). The survey provides the broadest geographical coverage of all of the sampling programs. Although this survey is focused on out-migrating juvenile salmon, YOY splittail disperse from spawning grounds in May and June and are captured effectively by the beach seine. Sampling was conducted 1976-1984, but was only consistent from 1979-1983 and again 1992-present. The beach seine primarily captures YOY splittail but fish less than 25 mm long are not recorded because of difficulty of identification. The annual abundance index is calculated as the mean catch per haul by station and month, averaged for each subarea, then for each year, then summed across subareas using May-June beach seine data for "core" stations within each subarea. Previous indices based on these data (e.g., Sommer et al. 1997) gave all hauls equal weight; updated indices give all stations equal weight. The limited annual sampling shows low to moderate catches during dry years and higher catches during wet years (Figure 6). An even more limited data set (1992 to 2002) for the Sacramento River upstream of the American River confluence (not depicted in Figure 6) shows that the proportion of river-caught to delta-caught YOY increased in dry as compared to wet years such that over half the YOY captured came from locations outside the Delta.

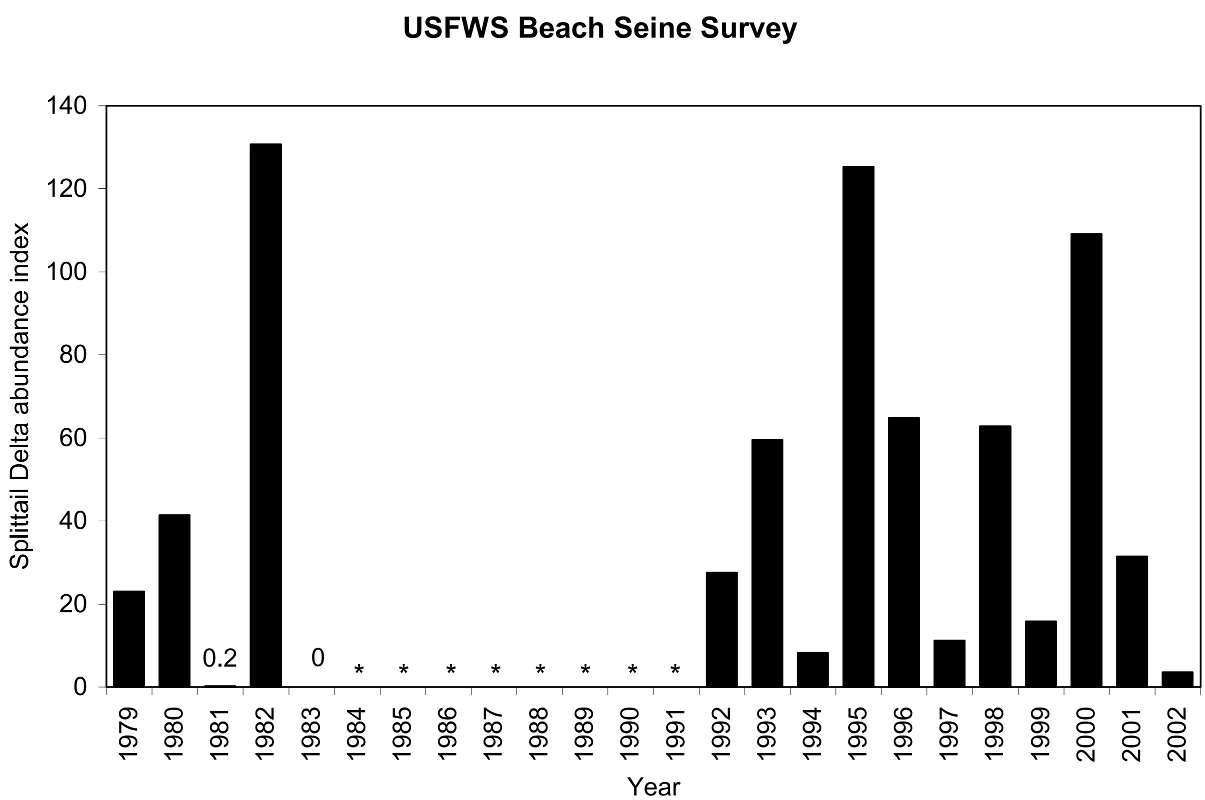


Figure 6. Splittail abundance index (see text for calculations) from the USFWS Beach

Seine Survey. An asterisk (*) denotes years in which no sampling occurred.

San Francisco Bay Study. The Interagency Ecological Program samples waters west of the Delta down to south San Francisco Bay using both a midwater trawl and an otter trawl (Sommer et al. 1997). It is considered important because it is a monthly sampling program and involves two gear types. The monthly midwater trawl index is calculated by multiplying mean catch per 10,000 m^3 for each embayment by the volume of each embayment, then summing the products. The monthly otter trawl index is calculated by multiplying mean catch per hectare for each embayment by the number of hectares for each embayment, then summing the products (Sommer et al. 1997). The annual indices are calculated as the average of the monthly indices with no consideration for missing data. Like all of the other surveys, there are a number of limitations in the use of the data to track splittail abundance trends. Specific limitations include:

- Catches of splittail are low. In the midwater trawl, YOY splittail appear in only about 5% of the trawls and older splittail are even less common. Mean annual catch for midwater trawl is 43 fish and for the otter trawl is 28 fish, and most are either YOY caught in a few years (1998, 1993, 1986, 1982) or yearlings caught in the following year. Thus, calculation of an "average" CPUE and subsequent expansion by the volume or area of an embayment is unrealistic.
- Much of the sampling takes place in deep water channels that are not characteristic splittail habitat.
- All splittail were caught in the Delta, Suisun Bay, and San Pablo Bay.
- The program missed many months of sampling between 1989 and 1999, resulting in incomplete seasonal and geographic coverage (J. Rosenfield, personal communication, see "Notes"). Most of the missing data are from the winter months (November-January).

Because these factors are all likely to greatly increase variability in the indices, decreasing their reliability, we use here a simpler measure, which is presence or absence of splittail in the trawls. Frequency of catch reflects both the abundance of the fish and the broadness of their distribution (J. Rosenfield, personal communication, see "Notes"). We present here only the results from the midwater trawl catch, because catches were higher and patterns were similar to the otter trawl catch. Also, only trawls conducted in San Pablo Bay, Suisun Bay, or the Delta are included because these are the only places where the midwater trawl caught splittail. Similarly, we present data from only the summer months – the longest continuously-sampled months in which splittail were collected by the midwater trawl (May-July for YOY and Apr-July for older splittail). The patterns of catch in either YOY (Figure 7) or fish one year or older (Figure 8) do not reflect any strong trends. YOY were caught in 12 of 21 years but catches were most frequent (10% of trawls or higher) in wet or above normal years (although not all wet years): 1982, 1986, 1995, 1998, 2000. YOY catches were consistently infrequent during the years of extended drought (1987-1992). Catches of older fish were infrequent in all years, with trends reflecting mainly the presence of a few strong year classes.

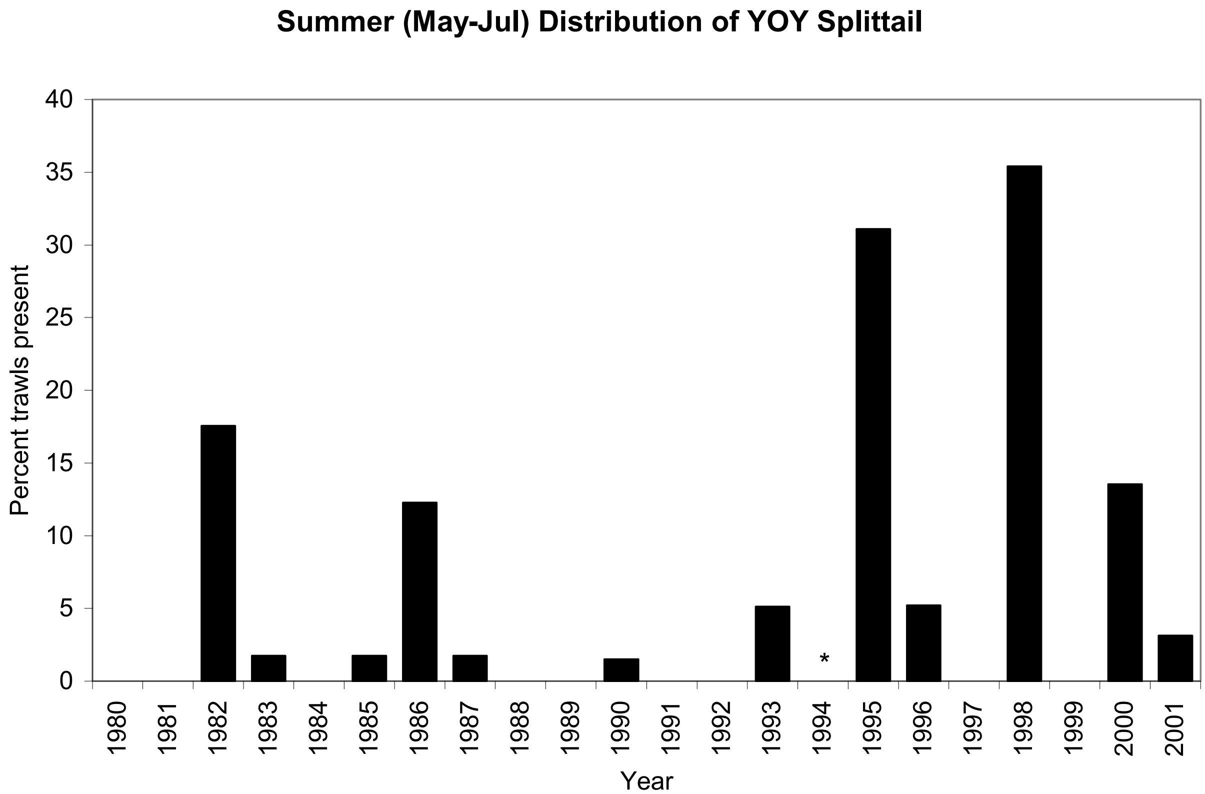


Figure 7. Percentage of midwater trawls containing YOY splittail from the CDFG Bay Study. 1994 is not included because of inadequate sampling. Percentage reflects all samples (across months and including sampling sites that were added as the sampling program continued) conducted May-July in the three embayments where splittail have been detected.

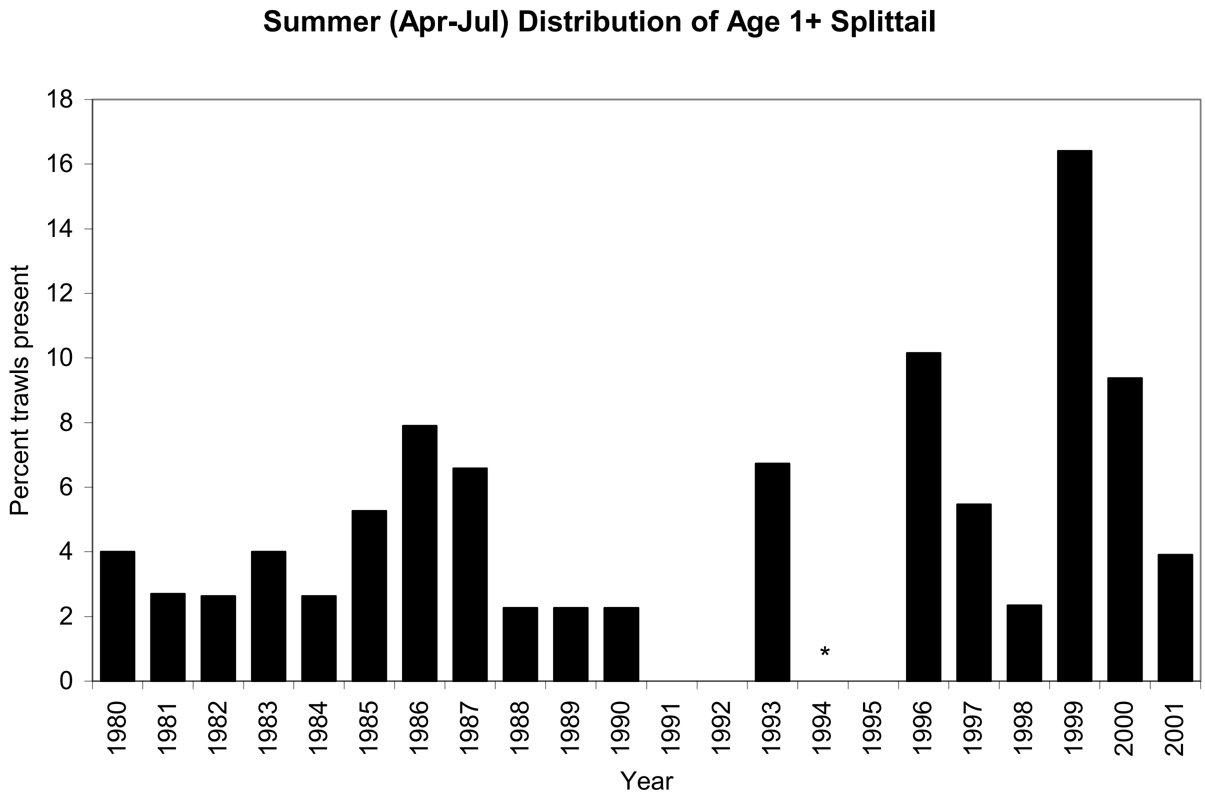


Figure 8. Percentage of midwater trawls containing Age 1+ splittail from the CDFG Bay Study. 1994 is not included because of inadequate sampling. Percentage reflects all samples (across months and including sampling sites that were added as the sampling program continued) conducted April-July in the three embayments where splittail have been detected.

Central Valley Project and State Water Project Fish Salvage. The Central Valley Project (CVP) and State Water Project (SWP) operate fish screening facilities to divert fish away from the pump intakes into holding facilities where they are counted and measured (CDWR & USBR 1994). Data collection takes place at 2-h intervals when the pumps are operating. Consequently, the fish salvage operations provide the highest number of splittail caught per survey, but number of data points (annual indices) is about the same as most other surveys (Sommer et al. 1997). Reliable CVP data and SWP data both start in 1979. The abundance index is calculated based on the total number of fish salvaged divided by the volume of water pumped (Sommer et al. 1997). However, the pumps are not operated as sampling programs *per se* so the amount of "sampling" is related to the amount of water exported, which in turn is related to the amount of water available, water demand, and, in recent years, changes in pump operations to protect migratory salmon and delta smelt (*Hypomesus transpacificus*) and to maintain appropriate salinities in Suisun Bay. Thus, comparisons with other sampling operations have to be made with caution. Nevertheless, the amount of water sampled is very large (typically 35-65% of all Delta inflow), resulting in the highest catch rates of any survey. Moreover, the general patterns are similar to other studies – nearly all the splittail collected are

YOY (especially in the CVP), with diminished catches during periods of drought and large catches following wet winters (Figures 9, 10).

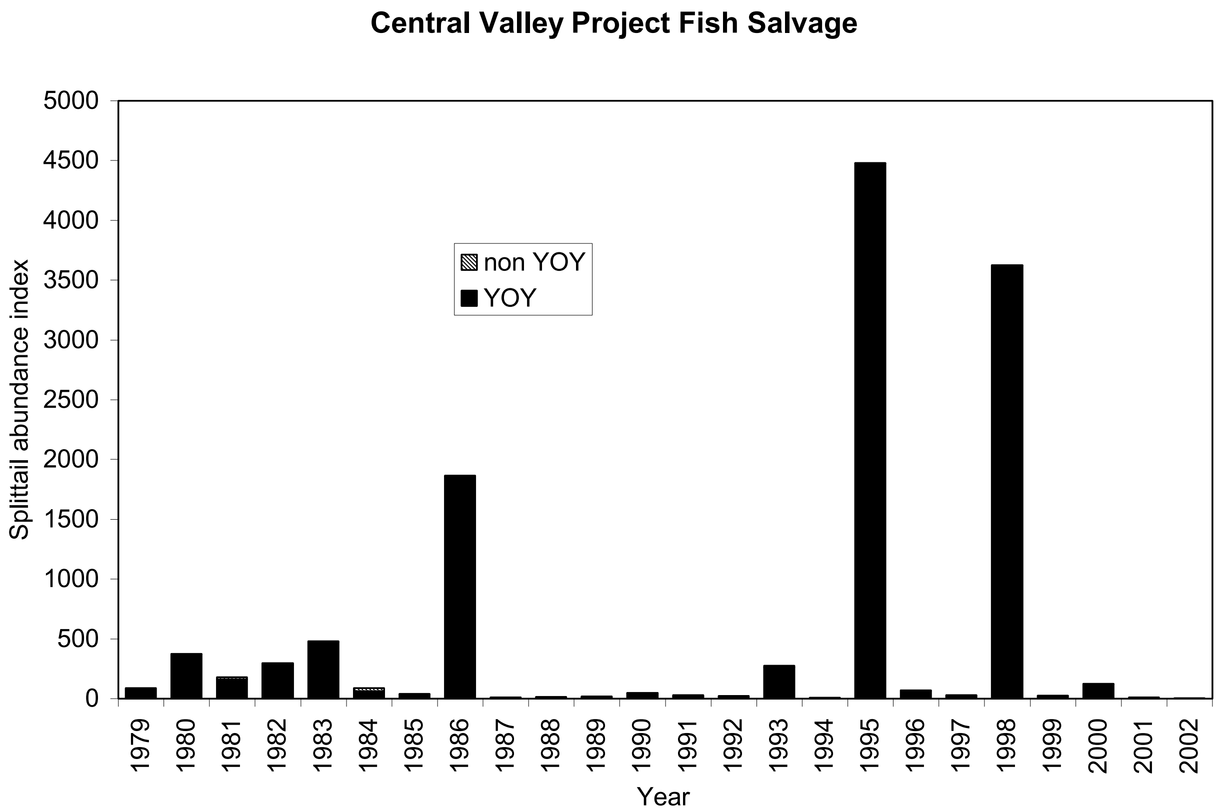


Figure 9. Splittail abundance index (see text for calculations) from the Central Valley Project fish salvage operation.

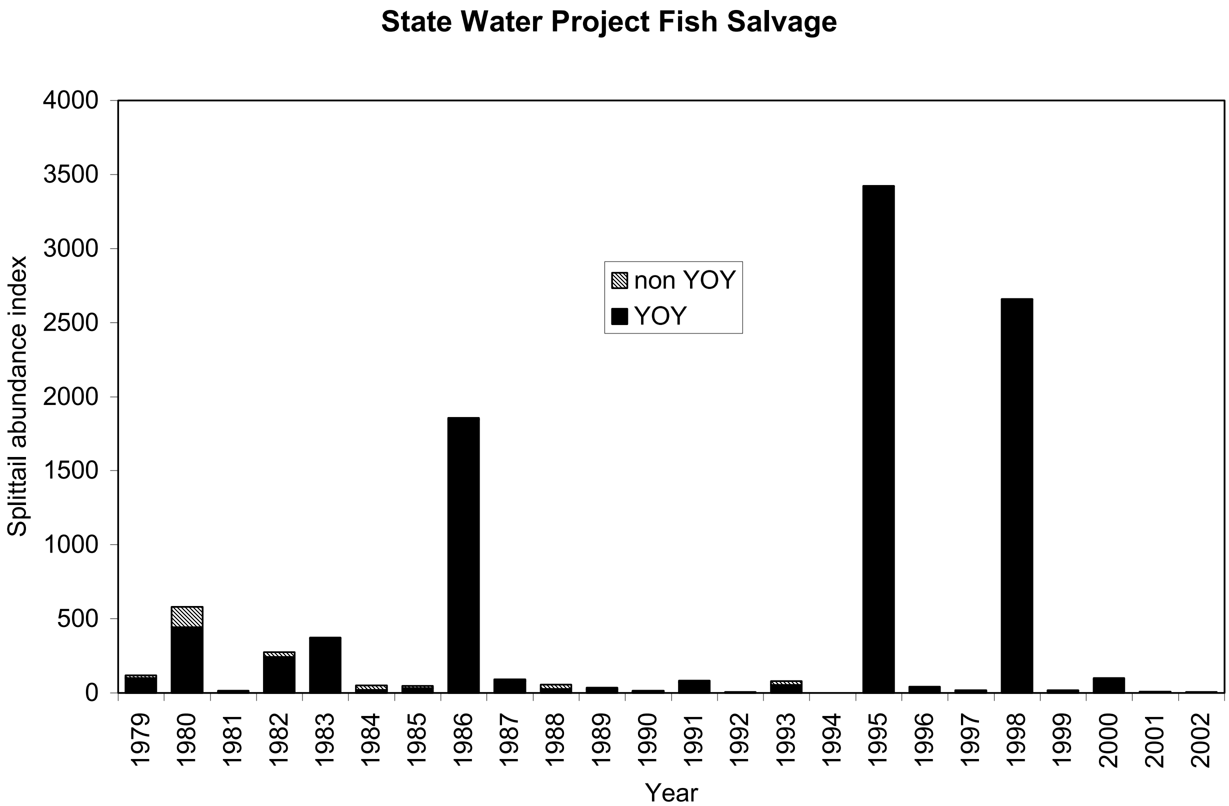


Figure 10. Splittail abundance index (see text for calculations) from the State Water Project fish salvage operation.

Conclusions. All fish sampling gear types and surveys suffer from selection bias that must be considered when interpreting results. Because none of the surveys were designed specifically to monitor splittail populations, the sampling gear, locations and frequency must all be taken into consideration when interpreting the data. All surveys sample YOY most effectively, so conclusions regarding YOY abundance are safest. The U. C. Davis Suisun Marsh Survey represents one of the most consistent sampling programs for all size classes. It shows a decline in splittail abundance beginning with the onset of the drought years, followed by a rebound that began in 1995. However, this survey covers a relatively small geographical area in which little spawning occurs, which may partially explain why the enormous peaks in YOY abundance observed by most other studies in 1995 and 1998 were more subdued in the Suisun Marsh data. Combined, the surveys indicate that (1) splittail populations have high natural variability, a reflection of their life history strategy, (2) some successful reproduction takes place every year, and (3) the largest numbers of young are produced only during years of relatively high outflow. These findings suggest that the majority of adult fish in the population result from spawning in wet years and lowest numbers are produced during drought years. The distribution and timing of YOY in the surveys also indicates that most spawning takes place in the bypasses, along the lower reaches of Sacramento and San Joaquin rivers and major tributaries, and lower Cosumnes river and similar areas in the western Delta, although some spawning also takes place in the Petaluma River and presumably Suisun Marsh under certain circumstances. Data from

Suisun Marsh suggest that YOY from upstream areas rear in Suisun Marsh, where they remain until they reach adulthood.

4.0 Ecology and Life History

4.1 Habitat

Non-reproductive splittail are most abundant in moderately shallow (< 4 m), brackish tidal sloughs, such as those found in Suisun Marsh, but they also can occur in freshwater areas that have either tidal or riverine flow. Historically they were present in alkaline lakes and sloughs on the floor of the Central Valley. For a cyprinid, they are remarkably tolerant of high salinities and are regularly found at salinities of 10-18 ‰, although they are generally most abundant at lower salinities (Meng and Moyle 1995, Sommer et al. 1997). Salinity tolerance increases with size; adult splittail can tolerate salinities up to 29 ‰ for short periods of time (Young and Cech 1996). Temperatures at which non-breeding splittail are found range from 5 to 24 °C depending on season, but acclimated fish survive temperatures of 29-33 °C for short periods (Young and Cech 1996). They also survive wide fluctuations in temperature. Splittail of all sizes can survive low dissolved oxygen levels (< 1 mg O_2 l^{-1}). These tolerances make them well suited to slow-moving sections of rivers and sloughs (Moyle et al. 1982, Daniels and Moyle 1983). In Suisun Marsh, splittail are abundant in late summer when salinities are typically 6-10 ‰ and temperatures 15-23 °C (Meng et al. 1994, Meng and Moyle 1995). This relationship with environmental variables seems correlative rather than causative, though, and the increased catches in summer are due more to the reproductive patterns of splittail (i.e., YOY recruitment from upstream) than they are to behavioral responses to the environmental fluctuations (Matern et al. 2002), which are well within the physiological limits of splittail (Young and Cech 1996).

Juveniles (< 2 yrs old and < 170 mm SL) are most abundant in shallow (often < 2 m deep), turbid water, with tidal currents, often in narrow sloughs lined with tules and other emergent plants. They are strong swimmers, capable of sustained swimming at 3-6 body lengths per second (Young and Cech 1996).

In a small-scale study on a model floodplain (Sommer et al. 2002), YOY splittail were found to be associated with the lower portion of the water column. The smallest YOY (15-20 mm FL) were closely associated with edge habitat during the day and deeper-water habitats at night while larger YOY (28-34 mm FL) used a wider range of habitats during the day and night.

4.2 Diet

Splittail are primarily benthic daytime foragers (Caywood 1974). In Suisun Marsh in the early 1980s, splittail foraged on (in rough order of importance) opossum shrimp (*Neomysis mercedis*), amphipods (*Corophium* spp.), and harpacticoid copepods, though detritus accounted for more than half of the gut contents by volume (Daniels and Moyle 1983, Feyrer et al. in press). When *N. mercedis* became rare each fall, splittail was the only abundant native fish in the marsh that failed to switch to a different preferred prey type (Feyrer et al. in press). After the invasion of the overbite clam (*Potamocorbula amurensis*) in the 1980s, *N. mercedis* populations collapsed (Kimmerer and Orsi 1996) and mysid shrimp ceased being important in the diet, even though other, smaller mysid species partially replaced *N. mercedis*. In the 1990s splittail in Suisun Marsh still ate mostly detritus and the most important identifiable prey items were bivalves, cladocerans, and harpacticoid copepods (Feyrer et al. in press). In the Delta, splittail feed opportunistically on clams, crustaceans, insect larvae, and other invertebrates (R. Baxter, unpublished data). Significantly, detrital material typically makes up 50-60% (by volume) of splittail gut contents (Feyrer et al. in press), although whether it is consumed deliberately or mainly incidental to prey capture is not known. The nutritional value of the detritus in their diet is not known, although, given the quantity, it is likely to have some importance.

Splittail of all sizes > 50 mm SL consume primarily detritus (Feyrer et al. in press). In addition, smaller fish feed on harpactacoid and calanoid copepods (Daniels and Moyle 1983, R. Baxter, unpublished data) while larger fish feed on larger benthic invertebrates, especially bivalves and amphipods (Feyrer et al. in press). Mysids were formerly the most important non-detrital prey item for splittail but their dietary importance declined when mysid abundance crashed following the invasion of the overbite clam (Feyrer et al. in press). Larval and small juvenile splittail (< 20 mm SL) feed primarily on cladocerans (56% dry weight) and chironomid larvae (40%), and to a lesser extent on planktonic copepods and rotifers (Kurth and Nobriga 2001).

Splittail on spawning migrations will move into flooded areas to feed on earthworms and other terrestrial organisms (Caywood 1974). Rutter (1908) reported splittail feeding on loose eggs in areas where chinook salmon (*Oncorhynchus tshawytscha*) were spawning, although splittail are no longer common in such areas.

4.3 Age and Growth

Splittail, like other Central Valley cyprinids are relatively long-lived and reach fairly large sizes (for North American cyprinids). Analysis of scales indicates life spans of 5-7 years (Daniels and Moyle 1983) but analysis of other hard parts indicates that the largest fish may be 8-10 years old (L. Grimaldo, CDWR, unpublished data; R. Baxter, unpublished data). Both sexes reach about 110-120 mm SL in their first year, 140-160 mm in the second year, and 200-215 mm SL in their third year, growing about 25-35 mm per yr thereafter. They may reach over 400 mm SL but fish over 300 mm SL are uncommon. The largest and oldest fish are females.

Growth rates, especially in the first year or two of life, may be strongly dependent on availability of high-quality food, as suggested by changes in growth rate following the invasion of the overbite clam into the marsh in the 1980s. This invasion was followed by the collapse of *Neomysis* populations upon which splittail historically specialized (Feyrer et al. in press). When growth rates of three strong cohorts of immature fish (to year 2) in Suisun Marsh are visually compared, the growth rate of the 1980 cohort appears to be greater than that of the 1995 cohort, with the 1986 cohort showing an intermediate growth rate (Figure 11).

Because splittail in Suisun Marsh grow very slowly during the cool months of October-March (e.g., change in YOY SL = 10 mm), data for these months were pooled and used in preliminary analyses comparing splittail lengths from 1979-1986 ("pre-clam") with those from 1986-1999 ("post-clam"). Pre-clam YOY (n = 2113) were significantly larger than the post-clam YOY (n = 906) and pre-clam 1+ (n = 1105) were significantly larger than the post-clam 1+ (n = 267) (T-test, type 2, 2 tailed; S. Matern and P. Moyle, unpublished data).

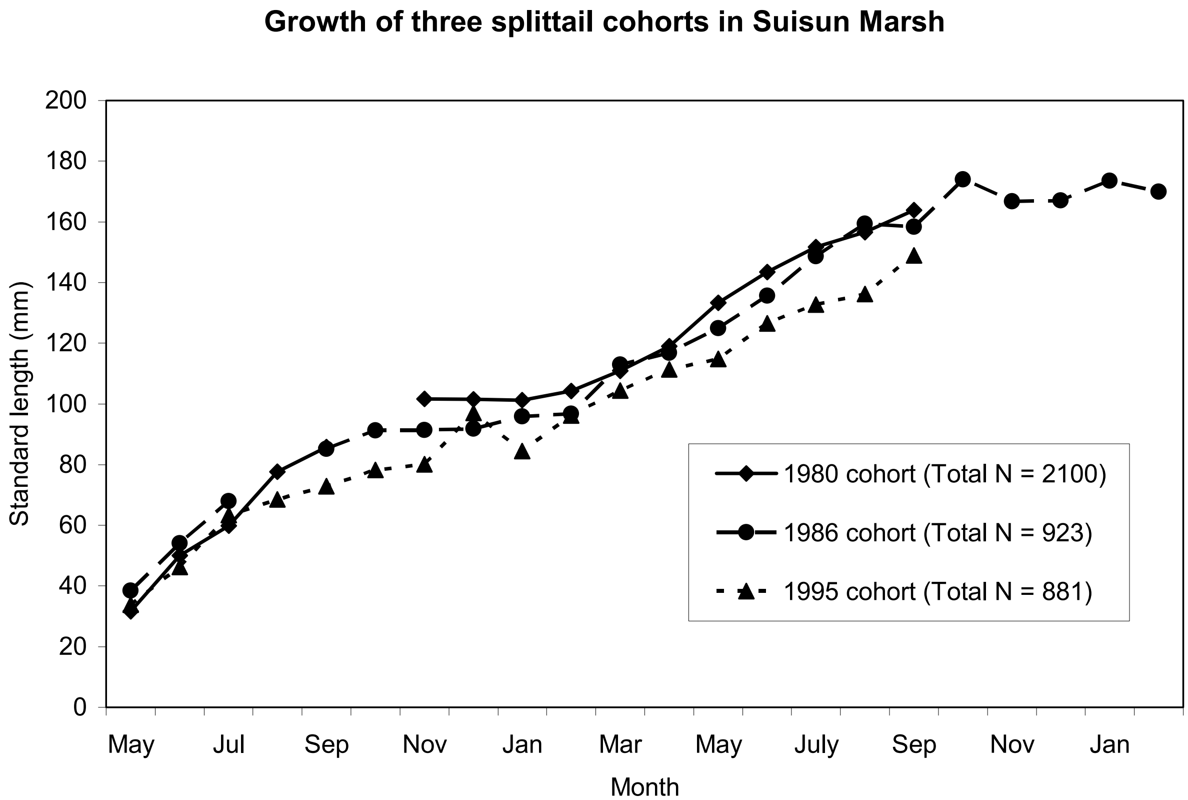


Figure 11. Growth of three cohorts of splittail for the first 22 months in Suisun Marsh , based on mean lengths from monthly samples from 1980, 1985, and 1995. S. Matern and P. Moyle, unpublished data.

4.4 Fecundity

Estimates of splittail fecundity (total oocytes) vary among studies. Caywood (1974) found an average of 165 ova per mm SL with a maximum of 100,800 in one female. Daniels and Moyle (1983) recorded an average of 600 ova per mm SL, with egg counts ranging from approximately 17,500 to 266,000 per female. Feyrer and Baxter (1998) found an average of 261 ova per mm SL with an estimated maximum fecundity of 150,000. Bailey et al. (2000), examining fish held for a considerable time in captivity, found that eggs made up an average of 12.3% of body weight and fecundity ranged from 24,753 to 72,314 eggs per female. The cause of this wide variability in estimates is uncertain, but fecundity may be related to food availability and/or selenium content of the increasingly important bivalve prey items (Feyrer and Baxter 1998, Feyrer et al. in press). For present populations, the best (most recent) relationship to use in provided by Feyrer and Baxter (1998): $F = 0.0004\ (SL_{mm})^{3.40}$.

4.5 Migration to Spawning Areas

Adults begin a gradual upstream migration towards spawning areas sometime between late November and late January. In a CDFG angler survey conducted at Garcia Bend (Sacramento rkm 80.5) and upstream, 1202 adult splittail were caught during 1991-1994 and 1999-2000; 94% of these were collected during the January-March migration period (R. Baxter, unpublished data). In 1998-99, four migration pulses were indicated by peaks in catch rate in an experimental fishery at Meader's Beach (Sacramento rkm 39) that occurred in mid-December, late January, and early February, and late February (Garman and Baxter 1999). The early (November-January) migrants were larger, with a median FL of 293.5 mm (*n* = 45), whereas later (February-March) migrants had a median FL of 273 mm (*n* = 64), supporting Caywood's (1974) observation that older fish may move upriver and spawn earlier than younger fish (Garman and Baxter 1999). Likewise, in state and federal fish salvage facilities in the south Delta, adults are captured most frequently in January through April when they are presumably engaged in migration to and from the spawning areas. The relationship between migrations and river flows is poorly understood, but it is likely that splittail have a positive response to increases in flows. Feeding in flooded riparian areas in the weeks just prior to spawning may be important for later success of spawning and for post-spawning survival. Not all splittail make significant movements prior to spawning, as indicated by evidence of spawning in Suisun Marsh (Meng and Matern 2001) and the Petaluma River.

The upstream movement of splittail is closely linked with flow events during February-April which inundate floodplains and riparian areas (Garman and Baxter 1999, Harrell and Sommer in press). Seasonal inundation of this habitat provides both spawning and foraging habitat for splittail (Caywood 1974, Daniels and Moyle 1983, Baxter et al. 1996, Sommer et al. 1997). Evidence of splittail spawning on floodplains has been found for both the San Joaquin and Sacramento rivers. In the San Joaquin drainage, spawning has apparently taken place in wet years in the region where the San Joaquin is joined by the Tuolumne and Merced rivers (T. Ford, personal communication, F. Ligon, personal communication, see "Notes"). Larvae and small juveniles have been found in Mud and Salt sloughs within Kesterson and San Luis National Wildlife Refuges (USFWS, unpublished data). Presumably, spawning took place in the flooded grasslands surrounding these sloughs. Spawning has also been documented on flooded areas along the lower Cosumnes River (Crain et al. in press). Spawning may take place elsewhere in the Delta (e.g., on mid-channel islands) but it has not been documented.

In the Sacramento drainage, the most important spawning areas appear to be the Yolo and Sutter Bypasses, which are extensively flooded during wet years (Sommer et al. 1997, Sommer et al. 2001a). However, some spawning takes place almost every year along the river edges and backwaters created by small increases in flow. Based on larval and beach seine sampling, splittail spawn in the Colusa to Knights Landing region of the Sacramento River in most years (R. Baxter, unpublished data, Baxter 1999a). Occasionally spawning can occur as far upstream as Hamilton City, as evidenced by sporadic collection of adult and YOY fish at a screw trap near the Glenn-Colusa Fish Screen (rkm 331). They apparently spawn in riparian vegetation adjacent to flooded rice fields in the lower 12 km of Sutter Bypass and in Butte Slough, based on the presence of numerous early-stage larvae during 1996, 1998 and 1999 (Baxter and Garman 1999, R. Baxter, unpublished data). Splittail may also spawn in the lower reaches of the American River when parts of the American River Parkway flood (R. Baxter, unpublished data).

In the Eastern Delta, the floodplain along the lower Cosumnes River appears to be most important as spawning habitat. Ripe splittail have been observed in areas flooded by levee breaches, in association with cool temperatures (< 15 °C), turbid water, and flooded terrestrial vegetation (P. Moyle, unpublished data).

4.6 Spawning Behavior and Habitat

As splittail become ready to spawn, their fins become tinged with red-orange and males become darker colored, developing tiny white tubercles on their heads and on bases of their fins (Wang 1995). Onset of spawning is associated with changing water levels, lower water temperatures, and increasing day length. In the Cosumnes River, they appear to move into flooded areas in late February or early March and then stay to spawn in March and April (Crain et al. in press) if the floodplain maintains appropriate depths and temperatures (< 20 °C). However, early flooding is not always necessary. For example, in 2003, when flows were only high enough to inundate the Cosumnes River floodplain in April, splittail were still able to spawn successfully and the larvae and YOY were collected in May (P. Moyle, unpublished data). Based on presence of larvae, spawning can apparently take place from late February to early July (Wang 1986, 1995). However, spawning after early May appears to be highly unusual. The largest and oldest females may reproduce first (Caywood 1974, Garman and Baxter 1999). The presence of several sizes of eggs in large females suggests they are fractional spawners, with individuals able to spawn repeatedly over several months (Wang 1986). However, in some years spawning may take place in a limited period of time; in 1995, a year of widespread and extraordinarily successful reproduction, most splittail spawned during a short period in April (Wang 1996). Splittail held in pens in Suisun Marsh became gravid at temperatures around 15 °C and salinities of 1.2 ‰ in mid-March; after a month, males ceased producing sperm but females remained gravid (Bailey et al. 2000). Females held in tanks indoors at constant temperatures of 18 °C did not mature, even with hormone injections (Bailey et al. 2000).

Complete spawning behavior has only been observed in captivity, but appears similar to that of other cyprinids; a ripe female swims over and through vegetation releasing eggs that are fertilized by one or more males swimming along-side and slightly behind (S. Teh, personal communication, see “Notes”). In this circumstance, spawning occurred the day after tank cleaning that included a drop in water elevation in the tank. Limited field observations indicate that, similar to other California cyprinids, males move into appropriate spawning areas and then waylay each ripe female in groups of 2-3 or more fish. Observations on the Cosumnes floodplain indicate that spawning fish move into open areas < 1.5 m deep that have dense growths of annual terrestrial plants; dead cockleburr plants may be especially favored because they provide shelter from predators and high flows and are a source of invertebrate prey (Crain et al. in press). Spawning areas are also characterized by the presence of flowing water, which keeps water temperature and clarity low (P. Moyle, unpublished data). In the Sutter Bypass, spawning sites were characterized by both annual and perennial vegetation, detectable water flow, and a water depth of approximately 2 m (R. Baxter, unpublished data).

Males are usually the first fish to enter flooded area and they may be last to leave, so would be particularly susceptible to predation and stranding. This may help to explain why few live more than 4 or 5 years. Post-spawning mortality due to parasites and stress-related disease may be common for both sexes. Post-spawning fish are often in poor condition and infested with anchor worms. Operators at the fish salvage facilities in the south Delta note that adult splittail caught during spring often have open sores on their sides. Presumably these fish are on their way back to downstream feeding areas.

4.7 Early Life History

Splittail eggs are 1.0-1.6 mm in diameter with a smooth transparent chorion (Wang 1986, Feyrer and Baxter 1998). Bailey et al. (2000) found that eggs weighed an average of 1.55-2.04 mg wet weight and had an average diameter of 1.38 mm. The eggs are demersal and adhesive (Wang 1986, Bailey 1994), attaching to submerged vegetation or any other submerged substrate. At 18.5 °C they start to hatch within 3-5 days after spawning (Bailey 1994). Eggs laid in clumps hatch more quickly than individual eggs. Larvae are 5.5-6.5 mm TL when they hatch, have a yolk sac, a non-functional mouth and no eye pigment (Wang 1986, 1995; Bailey et al. 2000).

At 5-7 days post-hatch, they reach 7-8 mm TL, the yolk is absorbed, and feeding begins, typically on small rotifers, (Bailey 1994). They switch to small crustaceans, then to dipterans as they grow larger (Kurth and Nobriga 2001). They reach 10-11 mm in 15 days post-hatching under laboratory conditions (Bailey et al. 2000). By the time they are 13-16 mm TL, they are recognizable as juveniles, with a swim bladder (Wang 1995). On the Cosumnes River floodplain, the early larval period seems to coincide with large blooms of zooplankton, providing an abundant food supply (Crain et al. in press). By the time they are 20-25 mm TL, they are easily recognizable as splittail and capable of fairly active swimming. Observations on small-scale floodplain wetlands indicate that the splittail are strongly associated with shallow edge habitat at a size of 20 mm, but gradually begin to use a variety of offshore habitats by 29 mm (Sommer et al. 2002). These early life history stages also appear to show strong diel differences in behavior; at night, many young become completely benthic. They stay on the floodplain to feed and grow as long as conditions are suitable (i.e., cool, flowing water is present). On the Cosumnes River floodplain in 1998, a year in which it stayed flooded well into June, juvenile splittail were common into May (K. Whitener, The Nature Conservancy, unpublished data). In 2000, most left abruptly over a short period in early May, when the floodplain was briefly reconnected with the river during two flow pulses produced by late rainstorms. Prior to the pulses, water had ceased flowing on to the floodplain and water temperatures had been steadily climbing.

On the Cosumnes River juveniles have been observed leaving the floodplain at a size of 25-40 mm TL, when they dispersed rapidly downstream (P. Moyle, unpublished data). In 2000, they were present in permanent sloughs adjacent to the Cosumnes River floodplain for only about two weeks after leaving the floodplain and were present in large numbers at the mouth on the Mokelumne River about 2 weeks later (P. Moyle and USFWS, unpublished data). This pattern has been seen elsewhere in the system. For example, large numbers of YOY splittail are typically captured in screw traps (set to at the base of floodplains) in the Sutter and Yolo bypasses in May, with diminishing numbers in June (CDFG, Region 2, unpublished data; Sommer et al. in press). YOY splittail are typically captured in large numbers at the SWP and CVP pumping plants in the south Delta in late May through mid-July, suggesting a seasonal downstream movement. By June and July, YOY splittail are present in marshes along Suisun Bay and in Suisun Marsh (Daniels and Moyle 1983, P. Moyle, unpublished data; C. Kitting, CSU Hayward, unpublished data).

The downstream dispersal of YOY splittail is now well documented and particularly evident after a wet spring. A less well studied aspect of splittail life history is the small fraction of YOY spawned in the Sacramento River and Butte Creek that remain upstream through their first growing season or first year (Baxter 1999a). Age-1 splittail have been captured moving down the Sutter Bypass in spring after rearing in Butte Creek or the Sacramento River (CDFG, unpublished data, Baxter 1999a). Additional YOY have been collected in the Sacramento River beach seine survey in fall and winter (USFWS, unpublished data; Baxter 1999a). There is little evidence for riverine rearing in the San Joaquin River.

5.0 Sources of Mortality

A key to managing any fish population is understanding sources of mortality, which vary among life history stages, and then separating natural mortality from mortality caused by human factors. For splittail, as for all fishes in the estuary, highest mortality rates from both sources are likely to be on early life history stages and tiny changes in mortality *rates* during these periods may have enormous effect on the number of adults appearing a few years later (Bennett and Moyle 1996). Another key factor that determines abundance of most fishes is egg supply, which in turn is related to the number and sizes of adult females. In this section, we discuss only sources of mortality affecting splittail under present conditions and do not address long-term sources of mortality such as loss of habitat.

5.1 Predation, Competition, and Disease

Most splittail that die of “natural’ causes are probably eaten by predators, although predation may only be the ultimate, not the proximate, cause of death. In other words, shortage of food, presence of competitors, or absence of refugia may force fish into habitats where the risk of being eaten is greater, increasing direct mortality from predation. Likewise, shortage of adequate cover in migration corridors or rearing areas may increase vulnerability to predation. Thus, while predation is a major cause of mortality throughout the life history of splittail, major predators and their impact on populations have not been determined, nor has the interaction of predation with other factors.

Larval and juvenile splittail in flooded areas are preyed upon by an array of invertebrate predators, as well as by juveniles of both native and alien fishes that invade the areas during flood events. If larval mortality rates are similar to those of other fishes, then it is likely that the vast majority of splittail die in their first few weeks of life at rates that are independent of densities of larvae but dependent on densities of predators and on stochastic environmental factors, such as sudden drops in water level that strand embryos and larvae. Water level may also affect predator density by expanding or contracting inundated habitat: expanded habitat should reduce predator (e.g., birds) density directly. In addition, most alien predatory fishes such as largemouth bass (*Micropterus salmoides*) and bluegill (*Lepomis macrochirus*) seldom venture far from permanent water courses (P. Moyle, unpublished data).

Adult and juvenile splittail are preyed upon by piscivorous fishes and birds. Although uncommon in striped bass diets, their effectiveness as bait for striped bass has long been recognized by anglers, who fish for splittail in order to use them for bait. Presumably centrarchid basses, sunfish, and crappies (*Pomoxis* spp.) are important predators on juveniles as they leave floodplain rearing areas. Juvenile pikeminnow (*Ptychocheilus grandis*) and chinook salmon are common on the floodplain and may prey on larvae and small juveniles, but this has yet to be documented. Bird predation appears limited until water recedes and floodplains begin to isolate from main channels at which point fish are exposed to wading birds.

The degree to which competition for food and space could affect splittail remains poorly understood. Splittail year class strength is primarily affected by the frequency and duration of floodplain habitat (Sommer et al. 1997). Within wet years, the available habitat is vast, so competition for spawning are is unlikely. By contrast, in dry years much of the spawning habitat is confined to the edges of river margins, raising the possibility that competition could be an issue. With regard to competition for food resources, the introduction of the overbite clam and the associated major changes to the food web of the San Francisco estuary provided a good opportunity to examine this question. Explosion of the clam population after 1987 was a primary reason for the severe decline of mysid shrimp (Kimmerer 2002), one of the preferred foods of splittail (Feyrer et al. in press). It is therefore reasonable to expect that this could have affected splittail. The analysis in Figure 11 certainly supports this hypothesis; however, a detailed analysis by Kimmerer (2002) of the abundance trends of several fishes including splittail found no statistically significant reduction in splittail abundance after the introduction of the clam. This contrasted with other native fishes such as delta smelt and longfin smelt (*Spirinchus thaleichthys*), which did decline. The clam's effect on smelt abundance likely occurred during the larval period; for splittail this stage was often completed in the floodplains or rivers, upstream of the clam's influences, whereas for both smelt species larval rearing areas generally overlapped the clam's distribution.

Splittail are infested with the usual array of parasites but parasites seem to have negative effects only when fish are stressed from other causes. Thus post-spawning splittail may be more vulnerable to parasites and disease. In general, the specific effects of parasites and disease on splittail are not known.

5.2 Fishery

One of the least appreciated aspects of the splittail migration is that they are subject to a considerable but poorly documented legal fishery from November through May. Anglers catch splittail using earthworms and cut bait. Most fish caught are kept because they are prized as food fish in Asian cuisine. Incidental data collected during creel surveys for striped bass and salmon (K. Murphy, CDFG, unpublished data) suggest that at times hundreds of adult fish may be caught on a daily basis. It is possible the fishery could significantly reduce egg supply available for spawning by reducing the number of large females. However, a majority of fish caught are relatively small (15-25 cm TL) so may be mostly males (J. Hileman, personal communication, see "Notes").

5.3.1 Entrainment: Small Diversions

Because splittail migrate through the lower reaches of rivers and the Delta as both adults and juveniles, they are vulnerable to entrainment in the numerous small irrigation diversions in the Delta and in urban aqueduct intakes.

There are over 1800 agricultural diversions in the Delta, which can collectively divert up to 4,000 cubic feet of water per second, although they do not operate simultaneously (CDWR 1993). The extent of entrainment of splittail in these small unscreened diversions is not well known, nor is it known how location of intakes in the water column affects entrainment. The best evidence is from Nobriga and Matica (in press), who conducted a study on a small diversion at Sherman Island, part of the core of distribution of splittail (Meng and Moyle 1995). They found they relatively small numbers of splittail were entrained. This is consistent with studies on swimming abilities of adult and juvenile splittail, which suggest they would be relatively invulnerable to small diversions, especially those with low intake velocities (Young et al. 1999, Danley et al. 2002). Small juveniles are vulnerable to some of the larger diversions in the Delta, in part because they seek inshore areas, but entrainment losses may be low because they tend to move downstream when flows are still fairly high and diversion rates are low. For the most part, volumes of water taken for irrigation during juvenile migrations are low compared to the volume in the rivers, suggesting low entrainment rates. Vulnerability, however, presumably increases later in the season as flows decrease and irrigation diversion increases.

Entrainment of splittail in the North Bay Aqueduct and the Contra Costa Canal is not known but is assumed to be small, perhaps incorrectly, due to the location of the diversions at the ends of sloughs. Only small juveniles are likely to be vulnerable. The North Bay Aqueduct presumably could entrain YOY splittail coming off the Yolo Bypass, but numbers are likely to be tiny given the volume of water pumped relative to the amount of water coming off the Bypass when flooded.

5.3.2 Entrainment: Antioch and Pittsburg Power Plants

The cooling intakes of the Antioch and Pittsburg power plants take in large numbers of small fish, including splittail. The effects of the two power plants on splittail are not known because no studies on entrainment have been conducted since the late 1970s (CDWR and USBR 1994) and monitoring stopped in the 1990s (M. Thabault, personal communication, see “Notes”). Given the large volume of water pumped through these plants and their location close to important splittail rearing habitat, the number of juvenile splittail entrained is potentially quite large. While the intakes are screened, the effectiveness of the screens for splittail is not known. They may also concentrate splittail predators.

5.3.3 Entrainment: SWP and CVP Pumps

The big pumps in the south Delta, run by the State Water Project (SWP) and the Central Valley Project (CVP), entrain large numbers of splittail adults and juveniles. Fish deflected from the export stream (generally those over about 20 mm TL) by specially designed louvers are captured and trucked back to the estuary. Adults are salvaged primarily in December-March, presumably in relation to spawning migrations (up and down), while juveniles are salvaged mainly in May and June, while moving downstream. The extent to which the salvage represents mortality is not known. However, the following observations suggest that there may be fairly substantial mortality of entrained fish.

- Small splittail moving towards the pumping plants probably suffer high predation rates in the exposed channels. In particular, Clifton Court Forebay, just before the SWP pumps, contains a large number of predatory fish, especially striped bass, which consume small fish in large numbers. Thus entrained splittail, especially juveniles, may represent a fraction of the total fish moving towards the pumps.
- While splittail are physiologically hardy, at least some mortality must be experienced from handling and transport, including predation in the tanks. Small YOY splittail are presumably especially likely to die from stress when they occur in large numbers and are crowded in the tanks. Adult fish can have high survival rates during entrainment and have been reared in pens subsequent to entrainment (Bailey et al. 2000).
- Predation rates on fish returned to the river may be high because the fish would be disoriented, away from cover, and facing large predators (mainly striped bass).
- Adult fish entrained during the spawning migration are typically returned to downstream locations, in effect forcing them to begin their spawning migrations again. The stress of entrainment may also reduce energy reserves needed for spawning and post-spawning survival. Thus it is possible that entrained adult splittail are removed from the spawning population at least for that year.

Recently, the effects of diversions and fish screens on splittail have received some attention. Young and Cech (1996) found that YOY splittail had critical swimming velocities close to velocities found at large diversions. Later, a study was conducted to determine if exposure to fish screens increased splittail stress and mortality and to evaluate the role of pre-screen water velocity in these responses (Danley et al. 2002). These researchers found that YOY swam faster than previously thought, exhibited positive rheotaxis, and swam faster when water velocity was increased. Thus, they concluded that increased mortality at fish screens was not due to screen exposure. Interestingly, although most YOY were easily able to avoid the screen, 20-40% of fish in all treatments, regardless of water velocity, entered the bypass simulating "salvage" (Danley et al. 2002).

Overall, survival rates of splittail of different size classes moving towards the pumping plants or entrained by them are not known. They are likely to be low and until studies are done demonstrating otherwise, it should be assumed that a high percentage of juvenile fish salvaged in fact represent mortalities. For adult fish, it is reasonable to assume low mortality but a high rate of removal from the spawning population for the year, of salvaged fish. The following discussion is based on the unpublished analysis of splittail salvage in the SWP plant by T. Cannon, Fishery Foundation of California. While the two pumping plants show some differences in salvage times and rates, they both entrain splittail in a similar fashion (R. Fujimura, CDFG, unpublished data) so presumably the SWP analysis can suffice for both.

Adult splittail usually show abrupt increases in numbers in the salvage in January and February after the first storms increase outflow in pulses. Salvage often increases on the descending limb of the pulses. Numbers salvaged are highest during years of high outflow and when winter water exports are high or rising. Numbers are also likely to be highest 1-3 years after wet years that produced strong year classes of splittail (CDWR and USBR 1994). Thus actual numbers of adult splittail entrained appears to be a complex function of (1) adult population size, (2) amount of pumping during winter months, (3) timing of pumping in relation to the hydrograph, and (4) total outflow.

Juvenile splittail appear at the pumps every year but numbers vary enormously. The positive correlation between numbers salvaged and March outflow (CDWR and USBR 1994) strongly suggests that entrainment is largely a function of the number of juvenile produced by successful spawning in flooded areas upstream of the Delta, particularly in the San Joaquin River and perhaps the Yolo Bypass. Juveniles usually start appearing (i.e., they're large enough to avoid being drawn through the louvers and to be counted in the salvage) at the salvage facilities in numbers in mid-May (at 20-60 mm TL), with numbers peaking in late May to mid-June. During wet years, salvage may continue into July. While the salvage numbers generally correspond with times the fish are moving downstream, the numbers increase as outflows decrease and export rates increase.

During some years, the number of splittail salvaged can be very high. For example, in 1998, over 3 million splittail were salvaged in the two facilities, making up nearly 25% of all fish captured in that year (Arnold 1999). The fish were primarily juveniles moving downstream, reflecting the extraordinary success of spawning that year. Salvage rates at the CVP facilities averaged approximately 5.7×10^{-3} fish per m^3 (7 fish per acre-foot) pumped during June when many splittail were moving downstream toward the Delta. Salvage rates at both facilities were the highest in 1995 when over 5 million splittail, mostly YOY, were salvaged (Arnold 1999).

The question of whether splittail populations are affected by entrainment at the SWP and CVP was examined in three different ways by Sommer et al. (1997). In one analysis, they found that there was a significant positive relationship between splittail abundance and entrainment; this result is contrary to the hypothesis that entrainment has a negative effect. Second, Sommer et al. (1997) found that salvage did not explain a significant portion of the variability in splittail abundance after the overriding effect of hydrology (i.e. floodplain inundation) was removed from their model. Finally, they examined patterns of entrainment in different water year types to determine whether splittail might be especially vulnerable in dry years. Sommer et al. (1997) showed that splittail salvage was highest in wet years, when the population was most robust; losses were typically low in dry years. They contrasted their results with delta smelt and longfin smelt, which are entrained primarily when their populations are most vulnerable (i.e., dry years). They concluded that there was no evidence that the south delta export pumps had an important population-level impact on splittail.

In general, it cannot be demonstrated that the large number of fish entrained at the SWP and CVP plants has a large negative impact on splittail populations. On the other hand, Sommer et al. (1997) indicated that their evidence does not demonstrate that entrainment would never have a population level impact in the future. In particular, they indicated that entrainment might affect abundance in a dry year if the core of distribution of the species shifted to near the pumps in the south Delta.

5.4 Pollutants

More than 400 toxic chemicals registered for agricultural uses and a large number of contaminants from municipal stormwater and sewage outfalls enter the San Francisco Estuary (United States Environmental protection Agency, unpublished data). Agricultural sources are untreated and unmeasured but probably vary widely in concentration and composition in time and space (Kuivila and Foe 1995). Kuivila and Moon (in press) documented dissolved pesticide concentration in the Sacramento-San Joaquin Delta during April-June (1998-2000), a time period when young developing splittail were present. They found water samples to contain 2-14 pesticides. Although the measured concentrations were well below LC_{50} values for the individual pesticides, the combination of multiple pesticides and lengthy exposure duration could potentially have sublethal effects on splittail, especially during early larval or juvenile development.

There have been strong shifts in recent years toward newer types of contaminants and various regulatory efforts to reduce contaminant impacts have often generated shifts from one type of compound to another. Contaminant concentrations are often sufficient to kill invertebrates and larval cyprinids in bioassay tests.

While toxicity studies are lacking, there is a high degree of certainty that splittail are adversely affected by exposure to contaminants in the environment (Teh et al. 2000). Possible pollutants include heavy metals, pesticides, herbicides, and polycyclic aromatic hydrocarbons. Teh et al. (in press) found that diazinon exposure caused spinal deformities and decreased growth in young splittail in laboratory treatments. Contaminants in the sediments are potentially the greatest threat to splittail because these fish are benthic foragers and are found in shallow water near the bottom. However, contaminants in the water column are also a concern. Evidence suggests that toxins in sediments may have significant effects on the biota of the benthic environment, even at low levels (Elder 1988). Splittail reside in the shoals, where there is a greater risk of exposure to urban and agricultural runoff. Toxicity may be reduced in channel areas, where greater dilution and flushing occur.

Perhaps of greatest concern are possible effects of selenium. In a recent study, tissues from wild-caught splittail had selenium levels that were high enough to potentially produce physiological effects on the splittail, including reproductive effects. The data also demonstrate that a potential food source, the overbite clam, had relatively high selenium concentrations (Stewart et al., submitted). Adult splittail feed on overbite clams and because the fish are long-lived, they accumulate selenium to levels that might affect development and survival of eggs and larvae (Moyle et al. 2000). Feyrer et al. (in press) found that splittail diet was largely composed of detritus and bivalves (including overbite clams) following the decline in mysid abundance. A diet increasingly focused on bivalves, especially the overbite clam, has the potential to negatively influence the reproductive biology of splittail and other fishes because of the clam's role as a pathway for transferring high concentrations of selenium to upper trophic levels (Stewart et al. submitted). Feyrer and Baxter (1998) documented lowered fecundity of splittail during the late 1990s compared to the early 1980s, suggesting that this hypothesis merits further investigation. In another study, results from Deng et al. (2003) indicate that splittail fed high concentrations of selenium grow significantly slower and have higher liver and muscle selenium concentration after 9 months of dietary selenium exposure.

5.5 Alien species

Splittail have managed to persist in the estuary in the face of invasions of dozens of fish and invertebrates that might impact their populations. Their major predators are probably mostly alien fishes (centrarchids, striped bass) and some of their present prey are alien invertebrates (Feyrer 1999, Feyrer et al. in press). However, the overbite clam has affected food supplies (see section 5.1) and increased risk of toxicant problems (see section 5.4). Thus, actions that increase the abundance of alien predators and competitors or that bring in new species to the estuary that would further change the system could create problems for splittail. A major concern is the potential invasion of predatory northern pike (*Esox lucius*); if allowed to spread from Lake Davis on the Feather River (Plumas Co.), they are likely to become abundant in habitats used by splittail for rearing and spawning (Moyle 2002).

5.6 Changed Estuarine Hydraulics

In the past three decades, changed hydraulic conditions in the Delta have been associated with declines in a number of fish species but it is not clear if there is a direct cause-and-effect relationship, especially with changes in splittail abundance. However, altered hydrology (e.g., reduced floodplain inundation; see section 5.7) may affect spawning success and it is likely that a return to historic flow conditions would benefit native species such as splittail (Meng and Matern 2001). The increased movement of YOY into the Delta interior during years with low spring outflow may lead to (1) increased within-Delta entrainment, (2) placement of small fish in environmental conditions less favorable for growth and survival and (3) increased probability of their being affected by agricultural pollutants.

5.7 Impacts of Diversion to Storage

A little studied aspect of the state and federal water systems is the effect of diversion to storage behind dams on species that use floodplains for foraging and spawning. Juveniles and adults of most floodplain adapted species are probably not often stranded by artificial water elevation fluctuations, unless they are very rapid, but eggs and larvae cannot move with rapidly receding water. Present upriver storage (and discharge) capacity is sufficient to prevent floodplain inundation in most low outflow years. However, Shasta and Oroville dams are capable of releasing sufficient water to inundate the lower Sutter Bypass and river flood terraces, so could be managed to favor splittail. If water storage capacity is increased (e.g., by raising Shasta Dam) floodplain inundation frequency and duration in the Sacramento Valley is likely to decrease, unless some of the water is reserved for floodplain inundation.

6.0 Life History: A Conceptual Model

The following description is a conceptual model, which means that aspects stated as facts are often speculative, although each aspect is based on existing knowledge and is as accurate as possible (Figure 12).

The life cycle of splittail revolves around downstream rearing areas and upstream spawning areas and movement between them. The downstream areas must have an abundance of appropriate food, protection from predators, and adequate water quality. The upstream spawning areas must have sufficient inundation to attract spawning fish and remain flooded long enough to allow for spawning, incubation of embryos, and rearing of larvae and small juveniles.

Adult (mature) splittail are 2-9 years old. Most of their time is spent in shallow, soft-bottomed areas where invertebrates, especially benthic crustaceans, are abundant. Splittail are bottom-oriented rovers, constantly searching for patches of food. Growth rates and fecundity are influenced by the availability of suitable prey. In their second or third year of life, individuals become mature for the first time and in January-February begin moving upstream (Figure 12). Movement becomes more directed when flows in the rivers increase, flooding riparian areas into which the fish move to feed on earthworms and other terrestrial sources of energy.

In response to high flows in late February-March, adults seek out inundated areas for spawning. Spawning takes place over submerged plants to which the fertilized eggs adhere. Each female produces thousands of tiny eggs and spawning takes place repeatedly over a 1-4 week period. Depending on water temperature, the embryos hatch in 5-10 days and the larvae remain among the vegetation for another 7-10 d, feeding on zooplankton. After they have transformed into benthic-feeding juveniles, 20-25 mm TL, they start leaving the floodplain, following the receding water. If high flows continuously keep water flowing through the floodplain and temperatures cool, the juveniles remain and continue to grow until the water recedes and temperatures rise. A late-season pulse of water may stimulate emigration. Thus successful reproduction on floodplains appears to require (1) an increase in river flows to bring the fish to floodplain area 2-3 weeks before spawning, (2) further flooding to stimulate spawning, and (3) water flowing through the floodplain for 4-6 weeks after spawning to allow for development of at least one batch of juvenile fish that can escape to the main Delta. In short, moderate to strong year classes of splittail develop when floodplains are inundated for 6-10 weeks between late February and late April. Small patches of habitat along the rivers can provide for some spawning in non-flood years but the number of juveniles produced is low. Surviving post-spawning females leave the floodplain as soon as spawning is finished and return to downstream feeding areas. Males may stay on the floodplain until the last female has spawned. Juvenile splittail first move into sloughs neighboring the floodplains and then move downstream into shallow, turbid, and, preferably, brackish rearing areas where they remain for 1-2 years feeding on benthic invertebrates and organic detritus. Growth is rapid in the first year of life, to 12-14 cm TL. Maximum size is around 40-45 cm TL, sizes achieved only by females, presumably because of heavier mortality of males.

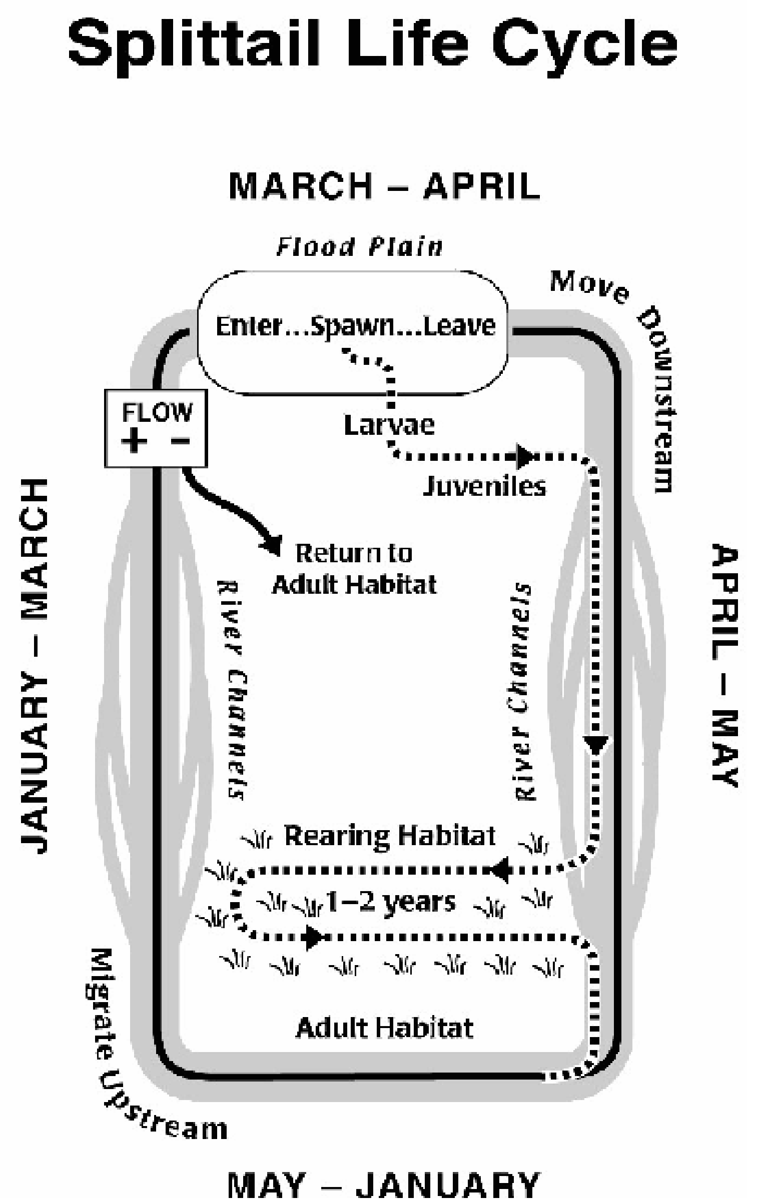


Figure 12. Conceptual model of splittail life cycle.

7.0 Uncertainties: Hypotheses on Life History Requirements

Although much has been learned about splittail biology in the past decade, many scientific uncertainties still exist and much of the data on splittail remains unpublished. In this section we present a series of hypotheses about splittail life history requirements as a way to indicate information needed to develop management strategies. The hypotheses are organized according to life stages and not according to importance.

H.1 Adult splittail migrate up river towards potential spawning areas every year regardless of flows (i.e., the migration is associated with gonadal development which is related to interactions of light, temperature, and nutrition).

Various sources of information indicate that every winter, adult splittail move up through the northern Delta and the lower Sacramento River. Annual movements into the San Joaquin River and southern Delta are less certain. The timing of this movement is not well understood and while some evidence indicates flow increases during winter can stimulate upstream movement (G. Garman and R. Baxter, unpublished data), other evidence suggests that high flows may not be necessary as long as suitable inundated floodplain habitat is available (Harrell and Sommer in press). Otherwise, splittail numbers in the Sacramento River peak in February and March immediately preceding and coincident with fish becoming ripe (Baxter et al. 1996, CDFG Region II, unpublished data). Laboratory studies (Bailey et al. 2000) indicate gonadal development is dependent on the natural pattern of daylight and is modified by nutrition. Gonadal maturation presumably generates hormones which trigger migration, as happens in many other vertebrates. While this general pattern seems reasonable, uncertainties exist in the timing of movement, the relative roles of external and internal cues in triggering the movement, and migration pathways. The upstream movement may also not happen for all adults in all years. In Suisun Marsh, for example, adults typically become scarce in January-March but in 2003 they remained abundant in all months (P. Moyle, unpublished data).

H.1.1 Higher flow levels in January and February lead to larger spawning runs.

The limited creel census data for splittail suggest increased catch in wetter years, consistent with a larger spawning run. A biologically reasonable mechanism for this hypothesis is that splittail may be attracted to upstream areas because they "smell" inundated soil or organic matter mobilized in high flow/precipitation periods.

H.1.2 Feeding in flooded areas along migration routes improves the condition factor of adults and associated egg production.

Adult splittail feed heavily on earthworms before spawning in wet years. It is possible that this energy source increases spawning success.

H.2 Splittail require seasonally inundated areas for spawning.

This hypothesis was first suggested by Caywood (1974) and is supported by strong correlations between timing and length of inundation of the Yolo Bypass (Sommer et al. 1997) and by direct observations of use of the Cosumnes River floodplain by splittail (P. Moyle, unpublished data). There is a great deal of information needed on what conditions bring splittail onto the floodplain and what conditions are best for spawning and rearing, as indicated by the following hypotheses.

H.2.1 Attraction flows are necessary in January, February, or early March to bring splittail in to spawning areas.

Early observations on the Cosumnes River and indicated that splittail do not move onto the floodplain when it first floods early in the season, but wait for 2-4 weeks before moving in as the hydrograph declines. If flooding is later (e.g., February), however, splittail may move on to flooded areas immediately. We do not know the size or duration of the initial pulse required to bring the splittail on to the floodplain. However, Harrell and Sommer (in press) found that relatively modest flow pulses (e.g., 18 $m^3 s^{-1}$) were sufficient to attract large numbers of splittail into Yolo Bypass. Delay early in the season makes sense biologically because zooplankton blooms may take several weeks to develop. Such blooms may be essential as food for larvae and juveniles. Evidence apparently contradictory to this hypothesis was presented by the limited spawning that took place on the Cosumnes River floodplain in 2003 (P. Moyle, unpublished data). In this year, there was virtually no flooding until late April and May. Presence of a few juvenile splittail stranded in floodplain pools in late May indicated that at least some spawning can take place late in the season. However, 2003 was also unusual because most adult splittail did not leave Suisun Marsh during the winter months (P. Moyle, unpublished data).

H.2.2 Spawning requires the right combination of temperatures, depth, water clarity, and current on the floodplain.

Studies on the Cosumnes River floodplain and Sutter Bypass are providing limited data on spawning requirements of splittail that show a relatively narrow combination of the four factors is needed. The requirements need to be determined in some detail in order to determine the best way to manage floodplain habitat.

H.2.3 Splittail prefer flooded annual vegetation for spawning.

It is known that the embryos of splittail stick to the substrate on which they are laid and that splittail spawn in areas of inundated annual terrestrial plants. However, it is not known if they can or will spawn on a wide variety of substrates and if large annual plants, such as cockleburrs provide the best spawning habitat. If splittail do spawn mainly on dead annual vegetation in open areas, then extensive restoration of floodplain forests may be detrimental to splittail spawning. Also areas of open, unshaded water tend to warm slightly and may produce plankton blooms better than riparian forest. In the Sutter Bypass, spawning took place in an area of mixed willow, annual grass, cockleburrs and other vegetation. A second spawning area was located in a band of riparian forest between the Sutter Bypass drainage canal and open agricultural land and included various annual plants, mature and immature cottonwood, hawthorn and valley oak. Until the importance of each habitat type can be clarified, the advice of Sommer et al. (2002) to provide a mosaic of floodplain habitat types in restoration projects seems appropriate.

H.2.4 During years of low winter flows, spawning can occur in marginal areas of rivers, in areas that are inundated annually for short periods.

In almost all dry years, some YOY splittail are captured in sampling programs particularly those sampling the Sacramento River (Baxter 2003). This suggests that large flows may not be absolutely necessary and some spawning can occur along river margins, in areas that do not require much increase in flow to be inundated. In addition, Sommer et al. (2002) demonstrated that splittail could successfully reproduce in a small, artificially flooded pond in the Yolo Bypass during a dry year. The exact location of natural dry-year spawning areas is not known, but their discovery would provide insights into minimum spawning requirements of splittail. The reach from Knights Landing upstream to Colusa and Ord Bend produces splittail in low outflow years and should be studied.

H.3 Splittail are fractional spawners.

Examination of ovaries indicates that female splittail have eggs in several stages of maturation, suggesting they are fractional spawners and spawn over 3-4 week (or more) period. However, field observations indicate they may deposit most of their eggs in a short period. If they are fractional spawners, individual females should remain in floodplain habitats for extended periods. Males should also remain, not only to mate with repeat spawners but to mate with females that arrive at different times.

H.3.1 Each female spawns several times during the spawning period in response to pulses of water in flooded areas.

Demonstration of this would require either recapturing marked fish or following sonic-tagged fish. Radio tagged splittail in the Sutter Bypass remained for 10-14 days before migrating downstream as the water level dropped in mid-March 1996 (R. Baxter, unpublished data).

H.3.2 Large females spawn earliest.

There is some indication that the largest females arrive in the spawning areas first, after the first males arrive (Garman and Baxter 1999). This may be related to their higher fecundity, which would give them more opportunity for protracted spawning or for taking advantage of the large plankton blooms that follow the first pulses on floodplains.

H.3.3 Males remain in spawning areas until all females have left, resulting in high mortality during and after spawning.

Male fitness is maximized by fertilizing as many ova as possible. Observations on the Sutter Bypass floodplain suggest that males remain longer than females; sex ratio of fish captured in groups strongly favors males (4-5:1) and males lose considerable weight. Both sexes contract external parasites (*Lernea* sp.) and secondary infections, but males may have a higher incidence of each. Prolonged spawning is presumed to exacerbate these problems.

H.4 Development of strong year classes requires extensive inundation of floodplains during March and April.

Evidence from both the Yolo Bypass and the Cosumnes floodplain suggest that strong year classes of splittail develop mainly following years when the floodplains are inundated continuously during March and April. In the Yolo Bypass, continuous flooding may not be necessary (e.g., 1995, 1998) as long as pond refugia are available between flood events and these events are not too widely spaced (T. Sommer, unpublished observations). Likewise, splittail reproduction may be increased by restoration projects that increase dry-year river-floodplain connectivity (Sommer et al. 2002).

H.4.1 Inundation must be continuous for 6-8 weeks to allow for spawning and rearing of early life history stages.

Laboratory and field studies indicate that development of new embryos to juveniles 20-25 mm TL requires at least 4-5 weeks, so multiple spawning by the same or new females in order to produce a strong year class presumably requires at least 6-8 weeks of flooding, possibly longer.

H.4.2 Inundation during January and February may bring splittail to the floodplain, but spawning does not occur until March.

Larval splittail apparently have been collected in February but there is little evidence of much spawning early in the season, even if the floodplains are inundated continuously. The reasons for this are not known, but may be related to cooler temperatures. The earliest time of major spawning is likely to be the last week in February. See H.2.2.

H.5 Larval splittail require flooded vegetation for rearing.

Studies on the Cosumnes River floodplain (Crain et al. in press) and in the Yolo Bypass (Sommer et al. 2002) indicate that splittail larvae are mainly found close to where they were spawned, in flooded terrestrial vegetation. Thus the larvae found in the Sacramento River may have been washed or drained out of preferred areas. The exact requirements for larval rearing, however, need to be determined.

H.5.1 Optimal temperatures for larval rearing are 17-20 °C.

These are the temperatures at which larvae have been observed on the Cosumnes River floodplain. Sutter Bypass temperatures and those of Great Valley Grasslands indicate that rearing continues on the floodplain at temperatures up to 22-24 °C, for larvae and small juveniles (R. Baxter, unpublished data). Observations in the Cosumnes River floodplain show that juveniles tend to leave the floodplain when small pulses from rain or snowmelt temporarily reconnect the floodplain with the main channel (Crain et al. in press). A combination of flow, depth, temperature and developmental stage may trigger emigration.

H.5.2 Water must be on the floodplain prior to the onset of larval feeding for at least two weeks, in order to allow dense populations of appropriate food organisms (rotifers and other microplankton) to develop.

Coincidentally this is about the time necessary for incubation. Dense plankton blooms occur on the Cosumnes River floodplain after initial flooding and these are presumably required for growth of larval and post-larval splittail. The exact relationship of these blooms to the success of splittail rearing is not known. In the Yolo Bypass, where there appears to be stronger flows through the vegetation, this relationship especially needs investigation. In the Sutter Bypass and the Cosumnes River, topography and vegetation act to laterally stratify water and create eddies: the shallower eastern edge of the bypass flows slower and the water becomes clearer and warmer than water flowing on the western edge. Increased temperature and improved water clarity are probably correlated with retention time and enhanced plankton development.

H.5.3 Survival rates of larval splittail are highest in vegetation of intermediate density.

Larval splittail are semi-planktonic and appear to occupy the spaces low in the water column (Sommer et al. 2002) around flooded plants, where presumably densities of food organisms are high and there is some protection from strong currents and predatory insects and fish (Crain et al. in press). When vegetation density is too high, larval fish may become trapped, especially if water recedes, but when it is too low, they may be more vulnerable to predation. This suggests that optimal conditions may be in patches of plants such as cockleburrs, which have a tree-like structure. Also, dense riparian forest may shade water, reducing phytoplankton/zooplankton growth.

H.5.4 Major sources of larval mortality are predation, stranding, and starvation.

Predation and starvation are typically found to be major sources of mortality in larval fish studies but their role for splittail is not known. Predation by alien fishes might be problem in some areas, as would stranding in human-made ponds and ditches.

H.6 Growth of juvenile splittail is fastest in floodplain habitats.

On the Cosumnes River floodplain, splittail can reach about 25 mm in six weeks after spawning. Fish that stay on the floodplain longer presumably continue to grow rapidly so are of larger size when they emigrate. Fish that are forced to leave at a minimum size presumably have slower growth rates outside the floodplain and higher mortality rates. Larger size presumably confers advantages to fish that have to move downstream through the Delta to brackish water rearing habitats.

H.6.1 Juvenile survival is better in floodplain habitat than in channel habitat because improved food resources lead to faster juvenile growth rates.

Studies in the Yolo Bypass (Sommer et al., 2001b) and Cosumnes River (P. Moyle, unpublished data) indicate that food resources are enhanced on floodplain habitat. It is very likely that this improves both growth and survival rates.

H.6.2 Juvenile splittail must reach ca. 25 mm TL in order to successfully emigrate to downstream rearing areas.

Fish of this size have been observed leaving the floodplain and are fairly strong swimmers. In both the Yolo Bypass and Cosumnes River, splittail may leave the floodplain at smaller sizes but then rear in associated channels until they reach 25-50 mm TL (T. Sommer, unpublished data, P. Moyle, unpublished data).

H.6.3 Juveniles from early spawning have higher survival rates.

These fish would presumably have a head start on taking advantage of zooplankton and midge blooms, have reduced predation (fewer predators on floodplain), and grow to larger sizes than later spawned fish (Sommer et al. 2001a, Crain et al. in press). They should thus leave the floodplain and its channels at larger sizes; this would be especially critical in years in which the floodplains are drained by early May.

H.6.4 Extended floodplain inundation improves growth and survival rates of juveniles.

Years in which there is continuous inundation through May may produce exceptionally strong year classes because embryos from protracted spawnings can hatch and grow and the juvenile rearing period for early hatchlings on the floodplain is extended, where they can continue to take advantage of high densities of food. However, this also provides additional opportunity for the later-spawning alien fishes to utilize the floodplain habitat (Sommer et al. 2001a, Crain et al. in press).

H.6.5 Predation by alien fishes is major cause of mortality of juvenile splittail both on and off the floodplain.

A correlated hypothesis is that high turbidity, associated with inflowing water, decreases predation and increases survival.

H.6.6 Survival of splittail on the floodplain is improved when complex habitat reduces water movement, allows warming and clearing in patches, and stimulates production of zooplankton and other food organisms.

There may be a strong relationship between hydraulics, habitat structure, food production, and larval growth and survival.

H.7 Juvenile splittail leave the floodplain in response to falling water levels (decreased depth, decreased currents, and increased temperatures).

Juvenile splittail appear to time their departure from the floodplain fairly precisely so they do not become stranded. What cues they use are not known, but it is likely that rising temperature is especially important.

H.7.1 Late season pulses trigger outmigration.

On the Cosumnes River floodplain in 2000 and 2001, late pulses of cool water that reconnected the floodplain to the main river following an extended period of rising temperatures were tied to mass exodus of juvenile splittail (Crain et al. in press). However, in Yolo Bypass it appears that pulses are not required for emigration when the floodplain is draining (T. Sommer, unpublished data).

H.7.2 Juvenile splittail follow drainage channels off the floodplain.

Natural floodplains had regular channels through them that presumably were passage ways for out-migrating splittail because they had the strongest currents.

H.7.3 Stranding is a major source of mortality in flooded areas mainly in artificial habitats that interfere with drainage or create permanent water.

Remarkably few adult or juvenile splittail seem to be left behind in floodplain pools in areas where there is good natural drainage to the rivers, often in the form of well-defined channels. In the Yolo Bypass, effective drainage is present due agricultural land grading (Sommer et al. 2001a). Significant stranding, however, may occur behind artificial structures which impound water, such as dikes, elevated roads, or levees. Stranding, followed by predation, may also be significant in permanent water on floodplains, such as ditches, ponds, and borrow pits.

H.7.4 Significant stranding of juvenile splittail occurs following sudden drops or fluctuations in flow.

In floodplains on regulated streams, sudden drops in flow created by water operations may not leave enough time or provide sufficient cues (e.g., rise in temperatures, gradual diminishing of flows or water level) for emigration to occur.

H.8 Most juvenile splittail, after leaving the floodplain, move downstream towards tidal or brackish areas for rearing.

In the estuary, there seems to be a steady progression of movement of YOY splittail downstream towards brackish water habitat in April-June but it is not known if this is directed movement or not.

H.8.1 Movement is strongly directed downstream by outflows and tidal currents.

H.8.2 The "movement" is an artifact of widespread dispersal and reduced habitat area because of diminished flows.

This is an alternative to H.8.1, but the apparent movement could be the result of a combination of the two factors. It is also possible that the apparent movement is an artifact of sampling programs that do not sample fish adequately in upstream areas. Screw trap sampling in the Sutter Bypass and beach seining along the Sacramento River indicate some YOY may spend several months to a year in upstream areas.

H.9 High mortality occurs in the downstream migration/movement of YOY splittail.

Splittail that have left the floodplain and are dispersing would seem to be exceptionally vulnerable to predation, entrainment, and other sources of mortality. It is important to determine if this is a life history stage that limits adult population size.

H.9.1 Entrainment in pumps of South Delta can be a substantial source of mortality during some water years, particularly if subpopulations of this species exist.

YOY splittail are entrained in large numbers by the SWP and CVP pumps and numbers appear to be related mainly to total abundance and successful spawning in the San Joaquin River. It is not known if fish entrained die either while entrained or while/after being trucked back to the Delta following salvage, although work by Danley et al. (2002) indicates that exposure to the screen does not significantly increase stress or mortality. It is also not known if fish lost through entrainment represent a significant segment of the splittail population (i.e. that their loss is reflected later in small adult populations), especially when populations are low. CDWR and USBR (1994) found that SWP YOY salvage was positively correlated (r^2 <0.65) with adult abundance two years later, suggesting that high entrainment levels of YOY does not strongly affect recruitment of strong year classes to the adult population. Sommer et al. (1997) also concluded that south Delta water exports were positively correlated with YOY splittail abundance. This is an artifact of the splittail outflow-abundance relationship (i.e., high flows lead to higher export rates and to protracted floodplain inundation that results in strong year classes) and contrasts with other native fish, such as delta smelt and longfin smelt, which experience their highest entrainment rates during periods of low outflow. As a result of these findings Sommer et al. (1997) concluded the SWP and CVP pumps do not have a major impact on splittail populations. It is possible, however, that entrainment effects could affect subpopulations (if they exist). For example, the south Delta pumping plants likely have a disproportionate effect on splittail in the San Joaquin River.

H.9.2 Entrainment in within-Delta diversions is a major source of mortality, including entrainment in irrigation diversions, the power plants at Antioch and Pittsburgh, the North Bay Aqueduct, and the Contra Costa Canal .

It is most likely that entrainment in these facilities is not a major source of mortality for splittail, but studies are still needed to confirm lack of impact, especially for the power plants. Studies are also needed to determine the extent to which migrating juveniles are entrained in small diversions and the extent to which such factors as diversion location, intake placement, and timing of pumping/siphoning affect entrainment, especially in dry years.

H.9.3 Predation losses are reduced where shallow water (< 1 m) edge habitat exists.

This could also be stated as: predation losses of YOY fish are least where there is sheltered habitat along their movement corridors and in rearing areas. It is possible, for example, that in the Delta the invasive aquatic plant, *Egeria densa* has an adverse impact on splittail populations by blocking access to inshore areas and by providing habitat for predatory centrarchids, mainly largemouth bass and spotted bass (*Micropterus punctulatus*).

H.9.4 Rapid passage of YOY splittail to rearing areas increases survival.

If YOY move out of floodplains in response to spring pulses of water, these same pulses may move them rapidly downstream to favorable rearing areas. Presumably, the faster the passage, the lower the mortality, especially in reaches where little suitable rearing habitat exits (see H.10).

H.9.5 Hydraulic connection of Suisun Marsh rearing areas to the Yolo Bypass enhances success of splittail spawning in the bypass.

Recent hydraulic studies by Dr. Nancy Monsen (Stanford University) suggest that much of the water draining the Bypass enters Suisun Marsh via Montezuma Slough. If YOY splittail take advantage of this, then passage to presumed rearing areas should be rapid, avoiding diversions and increasing survival rates.

H.10 Juvenile splittail (50-100 mm TL) require semi-open, shallow, 'edge' habitat for rearing.

Most juvenile splittail are captured in programs that sample water < 2 m deep, such as the USFWS juvenile salmonid program or the U. C. Davis Suisun Marsh program. The efforts are not concentrated on juvenile splittail, however, so it is not known precisely what their habitat requirements are.

H.10.1 Optimal habitat is < 1m deep, tidal, turbid, brackish, and soft-bottomed.

This characterization is based on observations in various sampling programs and feeding habits, but not directed study. The relative importance of the four factors is not known, or if other factors are important as well.

H.10.2 Predation by alien fishes is the major source of mortality.

This would suggest a major reason for choosing habitats in H.10.1. Wading bird predation could be a factor in some shallow water habitats, particularly those isolated on a tidal basis.

H.10.3 Suisun Marsh and marshes on the south side of Suisun Bay provide good rearing habitat because of the combination of good physical conditions and low densities of alien predators.

Large numbers of YOY splittail have been found in these areas, so it is reasonable to assume they represent good conditions for rearing. It is also possible that this is suboptimal habitat that is used in years of high abundance because of the shortage of suitable rearing habitat elsewhere.

H.10.4 Lack of suitable rearing habitat in eastern and southern Delta reduces success of spawning in Cosumnes and San Joaquin river areas.

These fish presumably have to reach Suisun Bay to grow to adulthood (a major untested assumption) and survival rates while in transit may be exceptionally high because of the open nature of most channels or lack of areas where rearing could take place above Suisun Bay. It is possible that entrainment in the CVP and SWP pumps may also reduce survival rates of YOY splittail originating from the Cosumnes and San Joaquin rivers.

H.11 Growth (and hence survival) of juvenile splittail is reduced by competition for zooplankton and mysid shrimp with introduced planktivores and filter feeders (e.g., overbite clam).

The main observations to support this hypothesis are that after the invasion of the overbite clam splittail fullness and niche breadth decreased (Feyrer et al. in press) and growth of splittail in the first two years of life in Suisun Marsh was apparently reduced (see section 4.3). However, Kimmerer (2002) found no evidence that abundance was reduced after the introduction of the overbite clam. The latest invader that may affect splittail populations is the Siberian prawn (*Exopaleomon modestus*). This shrimp is presumably predatory (on mysids), grows fairly large (40-60 mm carapace length), and is abundant in the fresh and brackish water habitats favored by splittail.

H.12 The optimal (preferred) habitat of adult splittail is channels of the estuary with significant current either from rivers or tides.

This hypothesis is suggested by the observation that in most years, highest densities are found in the northwest Delta, Suisun Bay and Marsh and the lower reaches to streams tributary to Suisun and San Pablo bays.

H.13 The most important food from a nutritional standpoint for resident adult splittail is mysid shrimp and other crustaceans.

This hypothesis is based on observations of splittail diets in the early 1980s compared to diets in the late 1990s.

H.13.1 Reduced mysid shrimp populations have resulted in reduced growth rates of adult splittail.

See H.11.

H.13.2 Reduced mysid shrimp populations have resulted in decreased fecundity.

This implies that quality and quantity of food can affect fecundity. Fecundity (and fertility) may also be affected by elevated selenium resulting from feeding on overbite clams (Feyrer and Baxter 1998, Feyrer et al. in press).

H.13.3 Detritus provides nutrition for maintenance but not growth in adult splittail.

Detritus by volume is the biggest part of the gut contents of splittail, even during periods of high mysid abundance (Daniels and Moyle 1983, Feyrer et al. in press), so it presumably has some nutritional benefit. Studies on other species (e.g., common carp, *Cyprinus carpio*) in which detritus is a major part of the gut contents indicates that while they have a net gain of energy from detritus, they do not grow well on it as a sole diet.

H.13.4 *Potamocorbula amurensis* will continue to increase in dietary importance of adult splittail.

The overbite clam has become very abundant in splittail habitats and it may be a significant portion of the adult diet. It is possible that it will become increasingly important in diets because of its availability.

H.14 There are at least three subpopulations of splittail (Petaluma, Sacramento, and San Joaquin).

It is possible that splittail on the two sides of the Delta may complete their life histories in partial isolation from one another, and at least during low outflow periods splittail in the Petaluma River complete their life cycle in isolation. The first component of this hypothesis is based on new evidence that water flowing out of the Yolo Bypass tends to stay on the north side of the Delta (in the Sacramento River) and be drawn into Suisun Marsh. Likewise, it is possible that splittail on the San Joaquin side, including those from the Cosumnes River area, move mainly down the San Joaquin River and rear on the south side of Suisun Bay (in Big Break and similar areas). It is also possible, if unlikely, that there are non-migratory populations of splittail in the Sacramento River (Sutter Bypass) and sloughs of the San Joaquin River.

H.15 Year class strength is set by time juveniles are 25-30 mm TL and have moved off the floodplain.

This hypothesis is based on the idea that in many fishes year class strength reflects a combination of the number of eggs actually spawned by females and the survival of embryos, larvae, and juveniles in first 6-8 weeks of life. This hypothesis would require that small differences in mortality rates of splittail on the floodplain or during downstream migration in different play a large part in variation in year class success (H.9).

H.15.1 Mortality rates are fairly even (constant) through size classes after the first summer.

Length-frequency data from Suisun Marsh suggests that mortality rates between age classes of fish of ages 2-5 are not drastically different from one another.

H.16 Stock-recruit effects may occur at low population levels or with low effective number of spawners.

While there is a logarithmic relationship between fecundity and size in females (up to a point) and while strong year classes should produce large numbers of eggs within 2-3 years, many factors affect the total egg supply and hence the stock-recruit relationship. These factors are those that affect growth, fecundity, and survival of females. However, Sommer et al. (1997) found there was little or no stock recruitment relationship for splittail. With the exception of Suisun Marsh, they found no relationship between number of adults and number of young produced in a given year. Nonetheless, the crude abundance indices for adults and juveniles are not sensitive enough to detect subtle effects. For example, it is possible that most adults spawn only in wet years, making available measures of adult abundance a poor indicator of spawning potential. In some years the effective egg supply may be reduced just because few females choose to spawn due to poor environmental conditions. It is also quite possible that stock-recruit relationships are important at low adult abundance levels but not at moderate to high population levels.

H.16.1 The fishery targeted on migratory splittail in winter-spring significantly reduces total egg supply available for spawning.

We do not know how many splittail are taken in this fishery every year, but the number is likely to be fairly high based on cursory review of CDFG creel survey data by the CDFG.

H.16.2 Dietary contaminants (e.g., selenium in the overbite clam) reduce viability of splittail eggs.

Increased levels of selenium in adult splittail suggest this might become a factor in the future.

H.16.3 Predation by alien piscivores significantly reduces the spawning population.

If this hypothesis is correct, then the decline of large striped bass should enhance splittail populations while the increase in largemouth bass or downstream expansion of northern pike should have a negative effect.

H.16.4 Diet significantly affects fecundity.

If the apparent reduction of splittail fecundity is real, then dietary changes may be a major causal factor.

H.16.5 Low population levels cause stock-recruitment effects.

As noted above, very low population levels could create a limited egg supply.

H.16.6 Splittail do not spawn every year, making it difficult to detect stock-recruit relationships.

8.0 Simulation Model of Splittail Life History Dynamics

The evidence presented here underscores the great uncertainty associated with splittail population dynamics. Section 7.0 highlights multiple areas of uncertainty in life history, environmental relationships, population estimation and population regulation. Those uncertainties require research, some of which could be relatively short-term and/or experimental projects (e.g., H.2.2). However, some require long-term data (e.g., H.1.1) and others are impossible to determine experimentally (e.g., H.9.1). The data requirements make a totally empirical solution to resolving the uncertainties in these cases unlikely.

Simulation models can play a vital role in resolving some of these uncertainties about splittail biology. Thus, one of the best ways to explore splittail population dynamics is to develop models that simulate population responses to hypothetical combinations of environmental conditions and vital attributes of splittail biology. Once validated, such simulation models can be used to conduct experimental analyses, especially when time or experimental intractability make empirical solutions difficult or impossible. Modeling is particularly useful for splittail because they are long-lived fishes with high year-to-year variability in survival and reproductive success. As a result, population trends are not only hard to predict, but interpretation of any trends detected is difficult, especially when the data are marginal in quality. A simulation model can 'experiment' with splittail population dynamics over multiple generations and suggest scenarios that are most likely to be detrimental or beneficial to the species.

In this section, we present the first splittail model constructed and some of its early results.

8.1 Model Structure

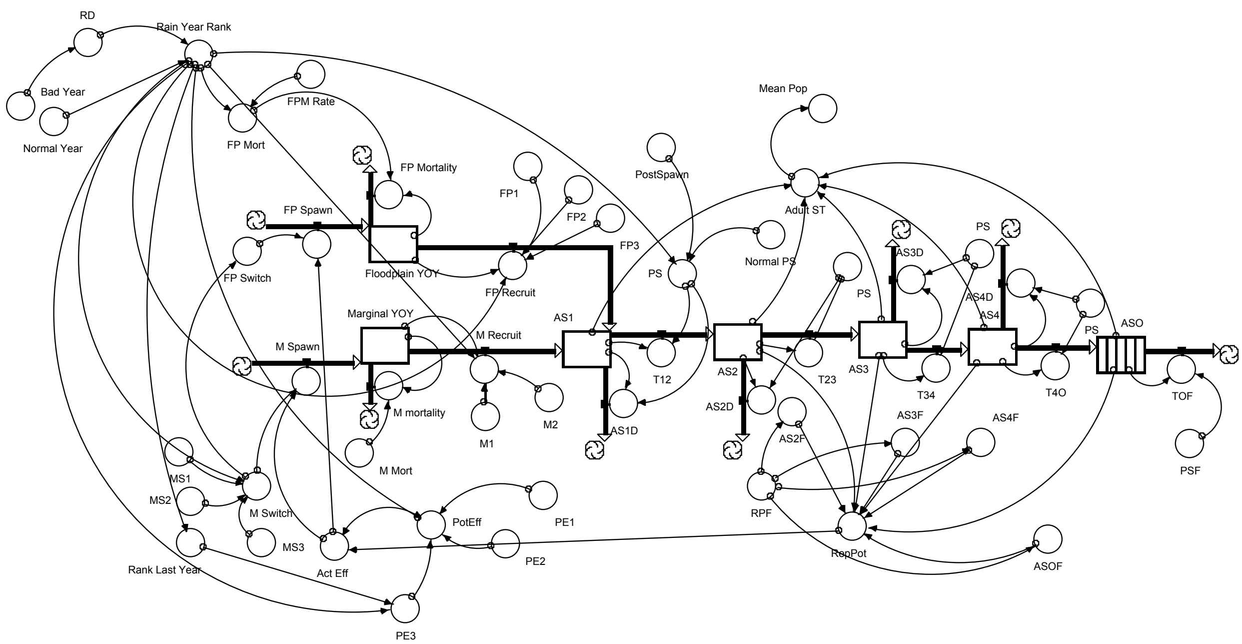
The model presented here was developed by T. C. Foin based on information presented in this document. The model is based on the known life cycle of the splittail (Figure 12). We have assumed that the environmental conditions most strongly driving abundance are the amount and duration of flows in rivers in the February-May period. These flows affect success of spawning and rearing in the flooded areas of rivers tributary to the San Francisco Estuary. This is the critical period when adult fish move upriver, assemble near spawning grounds, and choose how much to spawn and where. The model (*ST5*) was constructed using the STELLA simulation language, version 5.11. The basic structural relationships of the model represent a modified Leslie matrix formulation, based on age-size groups.

A complete diagram of the model is shown in Figure 13. The model contains two spawning strategies, one based on reproduction on riverine floodplains and other on more restricted spawning along river margins. The two are regulated by a logical switch (*FP_Switch*) which increases spawning effort and allocates the majority of spawning to the floodplain environment in wet and normal years and decreases it during dry years. *M_Switch* restricts spawning to river margins in drier years, but with minimal effort during wet and normal years. The number of YOY produced by each strategy is subject to different probabilities of survival (*FP_Mortality*, *M_Mortality*) and recruitment (*FP_Recruit*, *M_Recruit*). Survivors enter as subadults (*AS1*) and progress yearly through the remaining seven year classes (*AS2 ... ASO*) with a constant probability of survival by age (*PS*) until age 8, when all remaining survivors die. Ages 5 through 8 are aggregated because the numbers in each are small and do not warrant separate elaboration in the model. There is a provision for increased adult mortality in wet years, when there is apparently very high spawning effort (up to 90% of the adult female population).

Adult age-specific fecundity (*AS2F... ASOF*), multiplied by the numbers in each age class, determines the reproductive potential of the population (*RepPot*). The actual reproductive effort (effective fecundity) expended by the population (*Act_Eff*) is determined by the water year type (dry, normal, wet) which is based on empirical data from the frequency and duration of flooding in the Yolo Bypass (Sommer et al., 2001a). Actual reproductive effort is based on the fraction of females spawning in each year type (*PE1*, *PE2*, *PE3*). If there are back-to-back wet years, then the second year experiences reduced reproductive effort. Additional documentation of ST5 is contained in the notes at the bottom of Figure 13. These notes list variable names and their default values, which must be known for the reader to evaluate the baseline output of the model.

The model was constructed so that each of the vital attributes, behavioral switches and rainfall-flood drivers could be easily manipulated as simple changes in parameter value. In Figure 13, such inputs are converters without an input (i.e., circles with no arrow pointing to them). For example, *Bad_Year* is the probability that the current year will be dry. Its default value is 73%, but it can be reset to any feasible value between 0 and 100. By similar reasoning, the manipulable sectors are rain year (*Bad_Year, Normal_Year*), floodplain mortality (*FPM_Rate*), spawning effort (*FP_Switch*) and recruitment (*FP1*, *FP2*, *FP3*). Corresponding values for marginal YOY are *M_Mort*, *MS1*, *MS2*, *MS3*, *M1* and *M2*. Adult numbers are reduced following spawning by a combination of post_spawning mortality (*PostSpawn*) over the normal rate (*PS*). Losses of both YOY and adults are implicit and do not specify sources such as the fishery for migrating adults and to loss to the SWP and CVP pumps in the South Delta.

In the reproductive sector, the principal focus has been placed on the flood-year regulators of reproductive effort (*PE1*, *PE2*, *PE3*). Although the age-specific fecundity values are changeable in principle, we have generally chosen to accept their default values as reasonable and fixed, and to focus of survival processes instead.



User Documentation for Splittail V5: Vital Attributes and Environmental Parameters represented as scalars for easy user manipulation.
Bad Year: probability that water levels on the floodplains will be low. Default 73.
Normal Year: probability that there will be average flooding. Default 84 (default for wet years is 16).
PE1: fraction of females spawning in a low flood year. Default 0.001.
PE2: fraction spawning in a normal year. Default 0.10.
PE3: fraction spawning in a wet year. Two consecutive wet years: 0.10. Otherwise 0.90.
MS1: fraction spawning on floodplain margins in normal years. Default 0.20.
MS2: fraction spawning on margins in dry years. Default 0.40.
MS3: fraction spawning on margins in wet years. Default 0.05.
M1: surviving fraction of YOY moving down the estuary in wet years. Default 0.01.
M2: surviving fraction of YOY moving downriver otherwise. Default 0.001.
FP1: surviving fraction of floodplain YOY moving downriver in dry years. Default 0.0001.
FP2: surviving fraction in normal years. Default 0.001.
FP3: surviving fraction in wet years. Default 0.01.
FPM Rate: combined mortality of YOY on spawning grounds. Default 0.999.; in dry years 0.9999.
MMort: combined mortality of margin YOY. Default 0.9995.
PostSpawn: post spawning adult survival rate. Default 0.07. Normal PS Default 0.15. Fertility vectors are not meant to be manipulated.

Figure 13. STELLA flowchart for the splittail model (ST5). Rectangles are stocks (state variables), all representing age groups within the splittail population. The stock with vertical bars represents ages 5+. Flow between stocks is shown as double-width arrows. Circles and single arrows represent rate mechanisms regulating changes in stock size. The main groups in the model are related to reproduction, survival, and migration, in turn are regulated by outflow in any given water year. For further details, see the text and the boxnote, which lists variable names and default numerical values.

8.2 Baseline Output

The model closely follows the diagrammatic life cycle of Figure 12. With default parameter values and dynamics as described above, the model produces baseline behavior that varies with the random variables built into the water-year drivers. The basic dynamic pattern is shown in Figure 14. The potential fertility of each adult splittail is so high that even though "good spawning" flood years are infrequent, the resulting age classes are strong enough to guarantee population maintenance over a string of poor years. Put another way, the model suggests the large gain in a few good years more than offsets the losses of poor years.

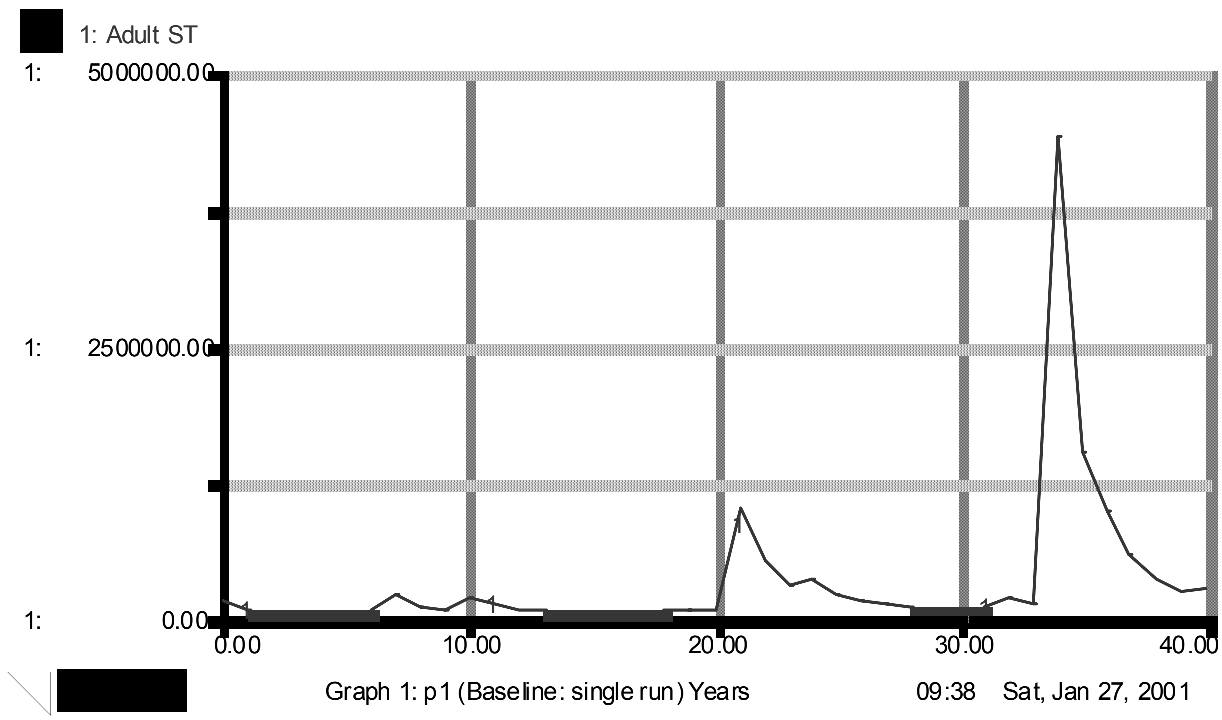


Figure 14. This graph illustrates the course of events when the model is run with its default parameter values, plotting splittail numbers over a 40-year period. Because this is a single run with a stochastic model, the results are representative but not the same as those from all subsequent runs with the same parameters. Population variability responds to annual precipitation, operating primarily through high spawning success on floodplains in wet years (see Figure 16). The model predicts that gradually building up the number of adults will eventually produce a large population when high total fecundity and a series of wet years intersect. The large peak 33 yrs into the simulation is typical.

The variability between years is more easily seen in a sequence of runs with the same parameters (Figure 15). The sequence of 10 runs shows one good year rising above the population trajectories of the other 9 years.

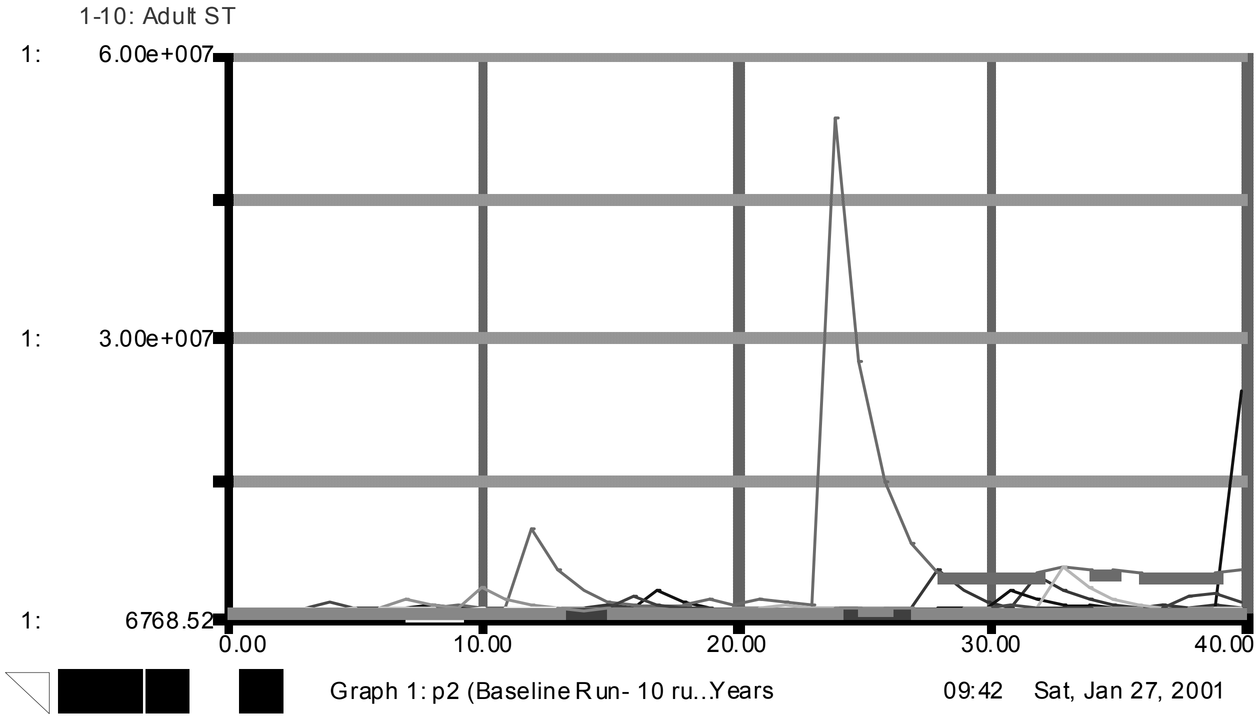


Figure 15. This plot of numbers of splittail vs year shows ten runs of the splittail model with the probability of a drought year fixed at 75%. Most runs display a sequence of low

population sizes (< 10^6 individuals total), but three populations show peaks in 12 to 40 years, illustrating the importance of wet years when the population has enough adult females to take advantage of them.

8.3 Results of Experimental Manipulation of the Model

The model has not been experimented with extensively, but the results to date support a number of tentative conclusions and suggest that the model may prove useful in developing a management program for splittail.

• **When conditions favor spawning over multiple years, the high reproductive potential of splittail supports very high population growth.**

This result is supported by the positive relationship between reproductive effort and flood year magnitude (Figure 16). There is a strong relationship between reproductive effort and population size, which is triggered by years with high precipitation. This is to be expected theoretically and is seen in entrainment numbers in the pumps of the south Delta.

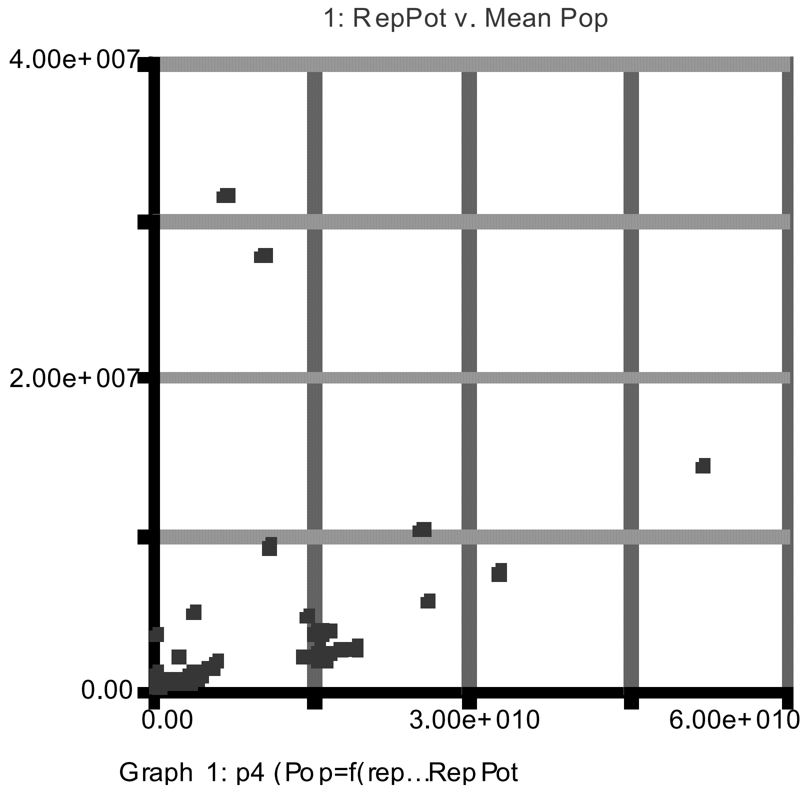


Figure 16. Scattergram of reproductive effort (total fecundity) as a function of mean population size. This plot suggests a direct relationship between the two variables, which represents the ability of splittail to produce large year classes when water conditions (i.e., floodplains inundated for a sufficient period of time) permit.

• **The ability of at least a few splittail to reproduce even under the worst flow conditions (presumably along river margins) insures that the population will persist indefinitely, despite downward trends in total population size during periods of drought.**

By changing Pr(bad year) to 1.00 and running the model for 40 years, we can estimate the effect of continuous drought on splittail population size (Figure 17). This graph illustrates the kind of experiment possible only with the model.

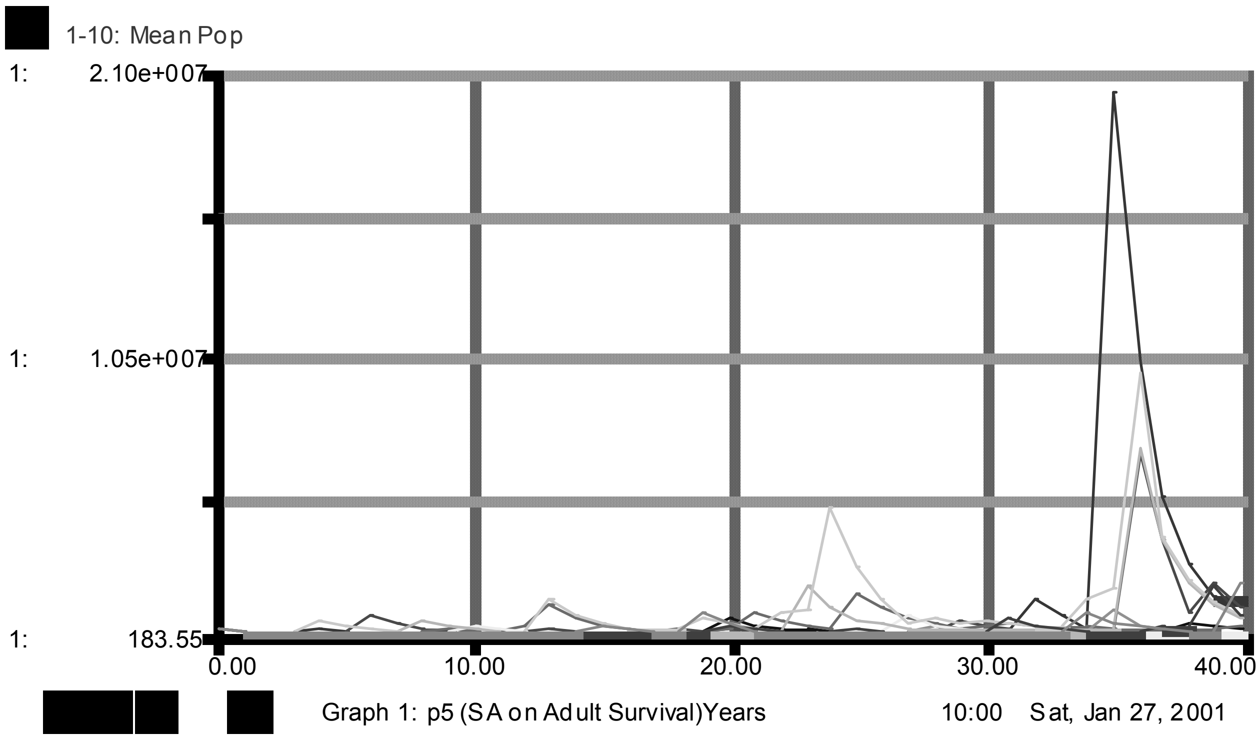


Figure 17. This graph shows ten runs of splittail population trends under the assumption that California experiences a 40-yr continuous drought. Most of the population trajectories are low with variation suppressed, but even under these unfavorable circumstances the slow accumulation of reproductive females eventually increases reproduction towards the end of the run.

• **Survival of splittail is not sensitive to low survival rates used in the model, reflecting that normal survival rates are probably low. In fact, raising survival probabilities of different life stages in the model increases growth potential far beyond anything observed in the wild.**

Sensitivity analysis consists of systematically changing an input (e.g., YOY survival rate) and assessing its effect on a response variable (e.g., mean population size). This particular example (Figure 18) illustrates the similarity of all population trajectories.

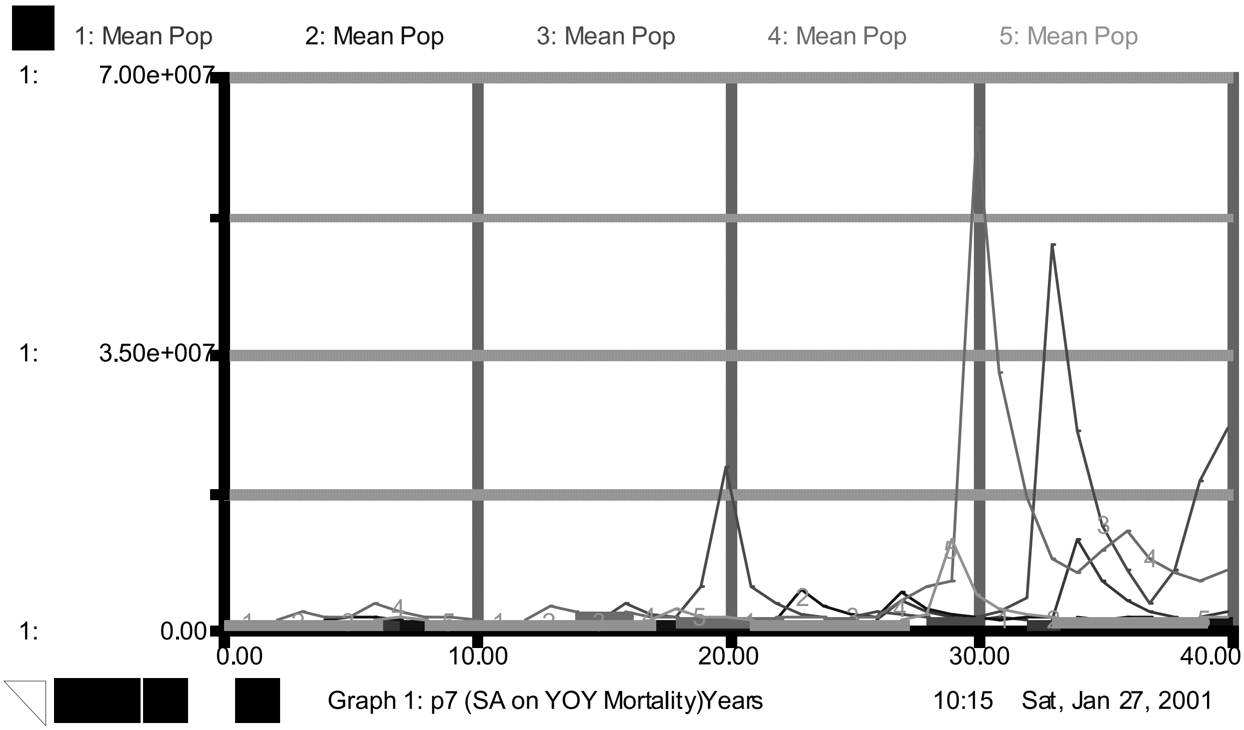


Figure 18. Sensitivity analysis of YOY survival, with a response variable of mean population size. YOY survival values range from 10% to 150% of normal. All curves are similar, suggesting that mean population size Y is not critically dependent on YOY survival (i.e., subsequent population size is not sensitive to differences in YOY survival).

• **Reducing female fecundity (i.e., relying on smaller females for spawning) has only a small effect on population growth.**

Figure 19 supports the conclusion that the high fertility of large adult splittail in good years generates enough population growth to sustain lesser years. It also argues that the population can be increased if conditions for good reproduction can be provided more often.

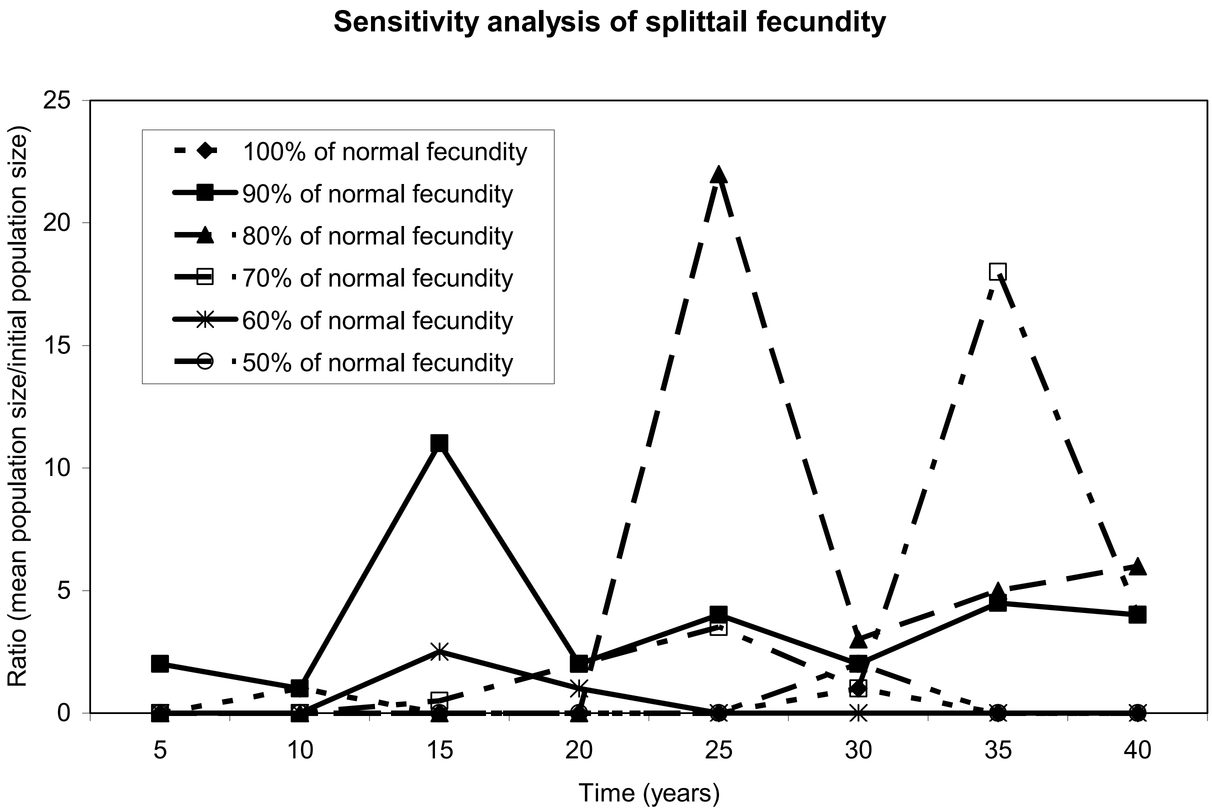


Figure 19. Sensitivity analysis of adult fecundity with a response variable of mean population size. Like Figure 18, this plot demonstrates that population variability is not correlated with fecundity level, suggesting that the number of adult females may be more important than individual fertility.

8.4 Conclusions

The results of many manipulations over various scenarios point to some conclusions which appear to be robust:

• Splittail populations have high variability with numbers that are driven in good part by annual spawning conditions, which in turn depend on rainfall. This is not surprising given that splittail are species with a life history pattern (high fecundity, fairly long life span, ability to migrate to suitable spawning areas) that indicates adaptation to a variable environment. This suggests that abundance in any one year, or even short-term decreases in abundance, may not be reliable measures of the species status.

• The population responds most strongly to years of high rainfall, which cause inundation of riparian areas for extended periods of time. In the model a succession of wet and normal years results in an exploding population, exceeding even what we have observed in recent years in the natural system. This is the result of interaction between adult numbers and reproductive potential under a string of favorable years. While this is a model flaw (in that unrealistic outputs are possible), curing it by imposing artificial population regulation is an unacceptable option, given the present state of our knowledge about factors limiting splittail numbers..

• While the model can be made to simulate population dynamics that mimic the natural situation, actual numbers for mortality and survival rates are lacking for the most part, so it is hard to distinguish among various sources of mortality. Nevertheless, the model can suggest which sources are likely to be most important because mortality rates can usually be bounded with reasonable numbers.

• The model indicates that a long series of dry years is unlikely to drive the splittail to extinction, even if the population is greatly reduced, as long as conditions not covered in the model do not change. The population seems to be able to maintain itself solely on marginal spawning, albeit with low numbers. For the most part, the impact of dry years is buffered by the ability of fish to spawn repeatedly, adult age structure, and high fecundity – the same factors that confer high potential population growth. Of course, a small population would be more vulnerable to unpredictable factors not modeled, such as a major pollution event.

• Increased adult mortality alone, from the combined effects of spawning, fishery, and diversions, has little impact on the population dynamics in the model.

• It seems reasonably certain that splittail numbers are naturally quite variable and that few conclusions can be drawn about population status from increases and decreases in the population. It follows that neither an increase to large, permanent population size or catastrophic declines threatening extinction will easily be detected with so much natural variation. Nevertheless, the model predicts that the potential for growth is larger than for extinction, barring a chronically small and concentrated population that would be subject to an environmental catastrophe.

8.5 Future Use of the Model

Improved confidence in the model can be developed with better measurements of various population parameters and by improving estimates of population size and variation. Especially useful would be better data on differences between survival of YOY on floodplains and along river margins from hatch through downstream migration. These refinements would permit more confident runs of the model of flow regime against survival and persistence of the population. Ultimately, there is a need to know how much site fidelity there is in reproduction to determine if the population is segmented and needs to be modeled as discrete subpopulations.

Certain experiments are possible with the model in its present form. A particularly attractive example is the evaluation of field projects, such as have been conducted by Sommer et al. (2002) on the Yolo Bypass. The model can build upon the positive responses of splittail in that study by estimating the population consequences of incremental increases (or reduction in variation) of reproduction, which in turn is linked to the duration and extent of flooding of the Yolo Bypass. The model can be used to evaluate the potential contribution of Yolo Bypass flooding regimes to splittail population dynamics and used as part of the design review.

A second example is the estimation of the consequences of loss of YOY splittail to the water export pumps in the South Delta. This use of the model will require the model to be sectored into spatial segments, given the emerging information of spatially-discrete population segments utilizing the northern and southern shores of Suisun Bay, the Sacramento River, and the San Joaquin River. Presumably the southern shore/San Joaquin segment has higher vulnerability to this source of mortality. The importance of pump mortality may then depend on the importance of the southern population segment to the mean population size and variability of the population as a whole. To the best of our knowledge, this has not been done previously, nor could it really be done without a model.

9.0 Global Warming and Earthquakes: The Big Gorillas

This paper, and most other documents relating to ecosystem management and recovery in the estuary, assumes that the basic configuration of the estuary will remain roughly the same for an indefinite period. In particular, such documents optimistically assume that the Delta will remain a system of freshwater channels and that Suisun Bay and Suisun Marsh will remain brackish water systems. Unfortunately, this is likely to be possible only as the result of major feats of engineering (e.g., dam across Carquinez Straits, tidal gates on all channels, strongly reinforced levees, etc.) and even the best and most expensive engineering may not be able to halt "natural" forces of change.

Global warming *is* occurring (Levitus et al. 2000, 2001) and it *will* have an impact on the estuary. The most severe impacts are likely to be through changes in precipitation patterns and rise in sea level. The most likely scenarios give northern California more water but most of it will come as rain and much less will be stored as snow in the Sierras. Year to year variability in precipitation will also be higher (as we are already seeing). This most likely means continued increase in large floods, increased frequency and severity of droughts, and increased difficulty of providing water for human and environmental needs. At the same time, sea level will keep rising due to melting of polar and glacial ice and thermal expansion of the ocean. A rise of 49 cm (19 in) in the next 100 years is the best estimate available of sea level rise, with a possible range of 20 to 86 cm (Warrick at al. 1996). However, processes by which heat is transferred from the atmosphere to the ocean is still being assessed (Levitus et al. 2001) and the role of large events, such as the 1997-1998 El Niño event, in dramatically heating the deep ocean are only beginning to be understood. It is possible that the effect of thermal expansion of the ocean is being underestimated. In the estuary, sea level rises will be amplified by tidal incursions into the narrow bays and channels because a greater volume of water will have to be squeezed into a relatively tight fixed space (Fisher et al. 1979). This rise will put enormous stress on all leveed systems in the estuary, but especially in the Delta, which is almost entirely below sea level already (and many areas are 5+ m below sea level). The resulting higher tides will likely stress levees in the Delta to widespread failure, turning the Delta into a brackish bay. Suisun Bay and Suisun Marsh will become increasingly saline, resembling San Pablo Bay as it is today. Salinities in the Delta and Suisun Bay, however, will show wide variability in response to increased floods and droughts. Coupled with the stress on levees caused by rising waters is the distinct possibility of levee failure and weakening in the next few years by earthquakes (Torres et al. 1999). Moreover, because the position of X2 (the 2 $\mu g\ l^{-1}$ isohaline line) is related to net Delta outflow, higher sea level and concomitant higher tides will push X2 further upstream, probably resulting in decreased primary and secondary productivity (Jassby et al. 1995).

Fortunately, splittail will probably be able to adjust to most of the changes because the historic Central Valley and its estuary, in which they evolved, have had enormous changes through the past million or so years, both in a geologic sense and in the sense of variability through time periods on the order of one to one hundred years. During periods of prolonged drought the Delta would have been largely a brackish water system; Suisun Bay would have been rather saline under the same conditions. Thus the migratory behavior of splittail can be viewed as an adaptation to fluctuating conditions. Somewhere in the system there would be both flooded areas for spawning and brackish areas for rearing. Thus under the changes predicted as the result of global warming, splittail could rear in the Delta and spawn in upstream flooded areas, such as the Sutter Bypass. They would be especially favored if levees along the Sacramento and San Joaquin rivers were set back to increase the amount of floodable land (as a way of increasing storage in flood-control reservoirs and countering the effects of sea level rise). The biggest problem they would face is likely to be the deep (3-6 m) water habitat that would dominate on flooded islands, which would be poor habitat for rearing. Thus their survival may hinge on having available large amounts of shallow tidal areas on the edges of the Delta.

10.0 Management and Restoration Options

Given the high fecundity of splittail and their ability to tolerate a wide variety of environmental conditions, the key to their long-term conservation is providing adequate spawning and rearing habitat and to preventing excessive mortality on upstream migrating adults and downstream migrating juveniles. Splittail populations are most likely to be severely stressed and depleted during a period of extended (7+ years) drought when spawning habitat is limited. This is also a period when pollution levels may rise (less dilution), diversions (as a percent of total outflow) are likely to increase, and salinities and temperatures rise, perhaps to stressful levels, in rearing habitats. Essentially, healthy (large) splittail populations require (1) flow regimes of inflowing rivers that result in periodic inundation of riparian habitats in lowland areas during winter and spring, (2) relatively safe migration corridors between spawning and rearing habitats, and (3) an abundance of brackish, shallow-water rearing habitat. An estuary with many of its natural habitat features restored would therefore be a good place for splittail. As always, it is important to make sure the management measures taken to enhance splittail populations are evaluated for potential effects on other species, native and non-native. The following options are both suggestions for research initiatives and suggestions for management; in the adaptive management frame work of CALFED, the two should go hand in hand. They are not listed in order of priority.

10.1 Improve estimates of splittail abundance.

The various fish surveys in the estuary together can be used to provide reasonably good indications of splittail abundance trends, especially for YOY. Individually, most of the surveys suffer from not being designed to sample splittail. The U. C. Davis Suisun Marsh survey most consistently collects all size classes of splittail but the trends for YOY are not always consistent with other surveys. There is thus a need to investigate either the development of a splittail-specific survey or to find ways to improve existing surveys to sample splittail better. For example, USFWS seining surveys could sample additional locations to better assess production in the rivers. Trawling surveys might be able to add stations in shallower areas or near splittail spawning areas. It might also be useful to develop an index of abundance of spawning (adult) fish. A mark-recapture program similar to that for striped bass would likely be the most accurate means to assess adult population size, but would be very expensive. A second approach involves verifying methods of aging splittail, then implementing a means of consistently sampling the adult population annually. By consistently collecting, sexing and aging fish over a short discrete period annually – such as during the spawning migration – over time the resulting data would allow determination of the relative size of each year class and its potential contribution to reproduction in each year. Although this information might not provide a good estimate of current population size, it would likely provide insights into factors influencing population trends and in particular the relative contributions of wet and dry year year classes to the population.

10.2 Protect and enhance remaining floodplains and flood terraces.

In recent years, as CALFED planned riparian restoration projects, the U.S. Army Corps of Engineers (ACE) has been proposing to clear and rip-rap sections of Sacramento River flood-terrace which presently support some of the last remaining riparian forests and splittail spawning habitat. Such areas may be critical for the limited spawning of splittail that takes place in dry years. Habitat restoration is too expensive to allow valuable habitat to be destroyed when other options may be available.

10.3 Provide additional access to floodplains.

Expansion of easily inundated floodplain habitat should enhance splittail reproduction and abundance, provided new areas are designed to drain properly and lack extensive areas of permanent water to harbor potential predatory fish.

10.4 Manage the Yolo and Sutter bypasses to benefit splittail and other native fishes.

The Yolo Bypass is clearly a major splittail spawning area and there is strong indication that even partial flooding for a sufficient period can result in successful spawning and rearing by splittail, even in dry years. Ongoing studies of splittail use of the Yolo Bypass should continue, including investigations of creation of spawning and rearing areas in non-flood years. Investigations should also continue on ways to improve the frequency and duration of flows through the bypass (e.g., with gates on the Fremont Weir) for the benefit of splittail and other native fishes. The importance of Sutter Bypass to splittail is less clear but it is likely to have some value for spawning and rearing. This needs to be documented better and ways found to manage the bypass to favor native fishes.

10.5 Continue to use simulation models to evaluate the population consequences of such as management of tidal and shallow floodplain habitat.

Potential impacts on splittail of diversions to storage and large, rapid reductions in dam discharge have not been evaluated although appropriate information has only recently become available (Sacramento and San Joaquin River Basins Comprehensive Study, ACE). GIS and survey data should be reviewed to identify floodplain and terrace locations potentially important to splittail. Models should then be run to determine critical flows for maintenance of inundation. Such information, could be used to assess potential impacts (e.g., drying up flooded areas) and to investigate alternative flow management strategies.

10.6 Provide additional channel margin habitat for juveniles.

Shallow margins of Delta channels appear to be important for migration and rearing of juvenile splittail. There is first a need for basic information on the kinds of habitat juvenile splittail use and how they use it, both seasonally and permanently. Means to increase suitable habitat then need to be determined, such as setting back levees, reclaiming islands as aquatic habitat, and breaching levees in marshy areas.

10.7 Provide additional brackish water rearing habitat for juveniles.

Recent studies suggest that shallow, tidal, brackish-water channels along Suisun Bay may be important rearing habitat for splittail. The characteristics of suitable rearing habitat need to be determined and incorporated into marsh restoration projects.

10.8 Evaluate losses of splittail at State and Federal pumping plants.

The pumping plants in the south Delta capture large numbers of splittail in all life history stages, especially in wet years when splittail are most abundant. It is not known, however, (1) what proportion of captured fish are mortalities, (2) if there are high mortalities from predation on fish drawn towards the plants, (3) if capture of adult fish affects their ability to spawn, and (4) if mortalities at the pumping plants has any impact on splittail populations.

10.9 Evaluate the effects of *all* sources of entrainment on splittail and develop (and implement) strategies to reduce entrainment mortality, especially in dry years.

Splittail larvae and juveniles are entrained not only by the CVP and SWP pumps but probably by the Antioch and Pittsburg Power Plants and other diversions in the Delta. There is still a need to understand what impact these diversions have, if any, on splittail populations. Impacts are most likely to be significant in dry years when a higher percentage of the water is diverted and splittail populations are depleted.

10.10 Reduce pollutant input, particularly of contaminants concentrated through the food web.

Recent evidence indicates adult splittail may be accumulating selenium in concentrations detrimental to reproduction, presumably by consuming the introduced overbite clam (R. Stewart, personal communication, see "Notes"). There is a need to investigate further the effects of selenium and other contaminants on splittail and to find ways to reduce sources. For example, alternatives to dispose of agricultural drain water from the western San Joaquin Valley include transport and dumping into Suisun Bay. Such an eventuality, without a similar reduction in industrial input, could result in impaired reproductive function in splittail.

10.11 Develop a management plan for the fishery on spawning migrants.

A fishery management plan should be established for splittail to limit the fishery impact on spawners. The fishery should be restricted during drought years.

10.12 Develop a systematic research program on the biology of splittail and other native resident fishes of the estuary.

The hypotheses in this paper indicate that there are many unanswered questions that bear on management. Particularly useful would be radio telemetry and marking studies to track migrations, to determine fidelity to spawning areas, to monitor survival of fish salvaged at the pumping plants and to locate important feeding and spawning areas. As battery technology improves, telemetry studies become more feasible. The information developed here needs to be used in hydrodynamic models of the estuary to determine if changes in flow regime affect movements of splittail between spawning and rearing areas. There is also a need for genetic studies to help determine if more than one population exists in the estuary.

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In an effort to be as comprehensive as possible, we list here not only literature cited in this document (12.1) but additional literature that was consulted but not cited (12.2), usually because it was redundant of or superceded by more recent reports or because it was too 'grey' to be citable (e.g., draft agency reports). These additional reports nevertheless contain useful information that can be used with caution. It is also worth noting that the frequently cited Interagency Ecological Program Newsletter is not a peer-reviewed publication although the articles were generally useful because they presented data summaries with minimal analysis.

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12.3 Notes

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